Factors influencing foraging decisions in ruddy turnstones Arenaria interpres (L.)

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by

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Abstract

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Animals must assimilate energy to survive and reproduce, but foraging conflicts with other demands on an animal's time. We know very little about how animals resolve these conflicts in natural settings. I studied foraging choices made by ruddy turnstones *Arenaria interpres* (L.) using rocky coastline in north-east England. In particular I explored how foraging decisions varied with resource quality, the predictability of patch appearance, and perceived predation risk while using alternative patches. This study includes the first quantitative investigation into the use of beach-cast wrack by shorebirds.

Energy intake per unit time by foragers on supratidal habitats was much higher than on intertidal habitats. However, birds exclusively used intertidal habitats when these were exposed by the tide, and moved onto supratidal habitats only over the high water period. Moreover, the number of birds feeding over a given high tide did not depend on supratidal food availability. These results suggested that there were costs to foraging supratidally. Were some foragers being forced to pay these costs because of low foraging efficiency, or did some accept the costs because of other associated benefits?

The use of supratidal habitats appeared to incur elevated predation risk for foragers; they were situated in areas where raptors could approach a foraging flock relatively closely before being detected. Accordingly, vigilance was much higher than expected on supratidal habitats, and increased with distance from the water's edge.

Birds that regularly fed supratidally tended to be males, older and higher-ranking, and had smaller, less patchy home ranges than birds that rarely fed supratidally. This suggests that some birds were paying the cost of elevated predation risk associated with supratidal feeding for the benefits of stable group membership and higher social status, while others minimised their need for supratidal feeding by spatially tracking the variation in intertidal habitat quality.

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"Enthusing students with his love of birdlife... He was directing his extensive research group, actively planning for future research, and being supportive to his students right to the end."

The Guardian, 18 December 2001

To my parents John and Jocelyn, and my sister Helen, whose continual sacrifices have enabled me to follow my dream

Chapter 1: General Introduction

Animals must assimilate energy to survive and reproduce. Foraging activities, however, frequently conflict with other demands on an animal's time, or expose it to risks to its survival greater than those posed by immediate starvation. The study of foraging in animals has had a long and controversial history, although a clear understanding of optimality rules and individual-based foraging choices is now beginning to emerge (MacArthur & Pianka 1966, Schoener 1971, Charnov 1976, Pyke 1984, Pierce & Ollason 1987, Stillman et al. 2000a, Uchmanski 2000, Railsback & Harvey 2002, van Gils et al. 2003). Foraging resources are often distributed patchily through the environment (Shorrocks et al. 1979). An individual's choice as to *where* it should forage will depend on the interactions of many potentially conflicting factors. Patch choice depends on patch quality, risk of predation, spatial and temporal resource predictability, physiological status and competitive ability (see Stephens & Krebs 1986 for a review).

This thesis reports work on a system in which foraging animals exploit high quality patchy and ephemeral resources within a matrix of low quality but more predictable resources. I attempt to unravel some of the costs and benefits associated with foraging on these alternative substrates, and investigate how foraging decisions in this system depend on resource characteristics, physiological status, social status and predation risk. The implications of anthropogenically-induced change in resource quality, namely a reduction in allochthonous nutrient input in the form of improved treatment of sewage effluent discharged into the area, are also considered.

Long-term studies on birds have provided much-needed empirical data that have thrown light on how animals choose foraging patches (Evans et al. 1984, Hunt 1991, Cody & Smallwood 1996, Goss-Custard 1996). Birds are mobile, amenable to captivity and experimental manipulation, and show measurable behavioural and physiological responses to variation in both the predictability and quality of foraging patches, and their risk of predation while

foraging on such patches. There remains, however, relatively little information about patch use under varying conditions in unmanipulated natural environments, yet a complete understanding of the ecological importance of alternative foraging patches depends partly on field study of appropriate model systems. The results of such field study will allow the formation of quantitative hypotheses for experimental testing.

1.1 Study system

I consider foraging choices made by ruddy turnstones *Arenaria interpres* (L.) on a stretch of predominantly natural rocky coastline in north-east England. This is an ideal model system for studying patch choice decisions by foragers under field conditions, because ruddy turnstones will use a wide variety of foraging substrates, and the choice of habitat at any one time for these birds is limited naturally by tidal oscillations. For example, supratidal habitats, defined here as those occurring above the most recent high tide mark, are available throughout the tidal cycle, whereas the extent of intertidal habitats varies greatly with tidal changes in sea level. The basis of this study, therefore, is to examine the distribution of foragers in relation to the changing availability and quality of intertidal and supratidal habitats.

Questions about the role of supratidal foraging in shorebirds have recently received some attention in soft-sediment systems (Goss-Custard et al. 1996, Caldow et al. 1999, Stillman et al. 2000b), but these habitats have radically different resource dynamics from the hard-substrate habitats studied here. In soft-sediment systems, individual oystercatchers *Haematopus ostralegus* (L.) of low foraging efficiency are more likely to use supplementary supratidal food supplies than individuals of higher foraging efficiency (Goss-Custard et al. 1996, Caldow et al. 1999, Stillman et al. 2000b). Intertidal substrates are inherently preferred, because the supplementary feeding areas are less profitable than intertidal substrates, and foragers use these marginal habitats only when the high quality intertidal habitats are unavailable. Soft-sediment coastal habitats are much more dynamic than rocky shore systems, with extreme spatial and temporal variation in physical substrate turnover and

recruitment patterns of invertebrate populations (Goss-Custard 1970, Evans & Dugan 1984). Moreover, recruitment is frequently affected by limited mixing and flushing in estuaries, so the system takes longer to recover from perturbation, and prey motility occurs in three dimensions either through prey movements or rearrangement of sediment by hydrological and weather conditions. Rocky-shore populations on the other hand are generally open, with rapid recovery from perturbation possible via recruitment from unaffected areas (Thompson et al. 2002), and invertebrate motility is necessarily two dimensional, the rocky substrate preventing burrowing. Does supratidal foraging play a similar supplementary role in these two systems with such radically different underlying resource dynamics?

To answer this question, I used this study system to explore how foraging decisions varied with resource quality, the predictability of patch appearance, and perceived predation risk while utilising alternative patches. In particular, I described and interpreted the use of supratidal beach-cast wrack[1] by ruddy turnstones (see section 1.1.2). Beach-cast wrack is a highly dynamic and potentially profitable foraging resource for shorebirds, although no study has yet quantified its importance or described its ecological role as a foraging substrate for shorebirds.

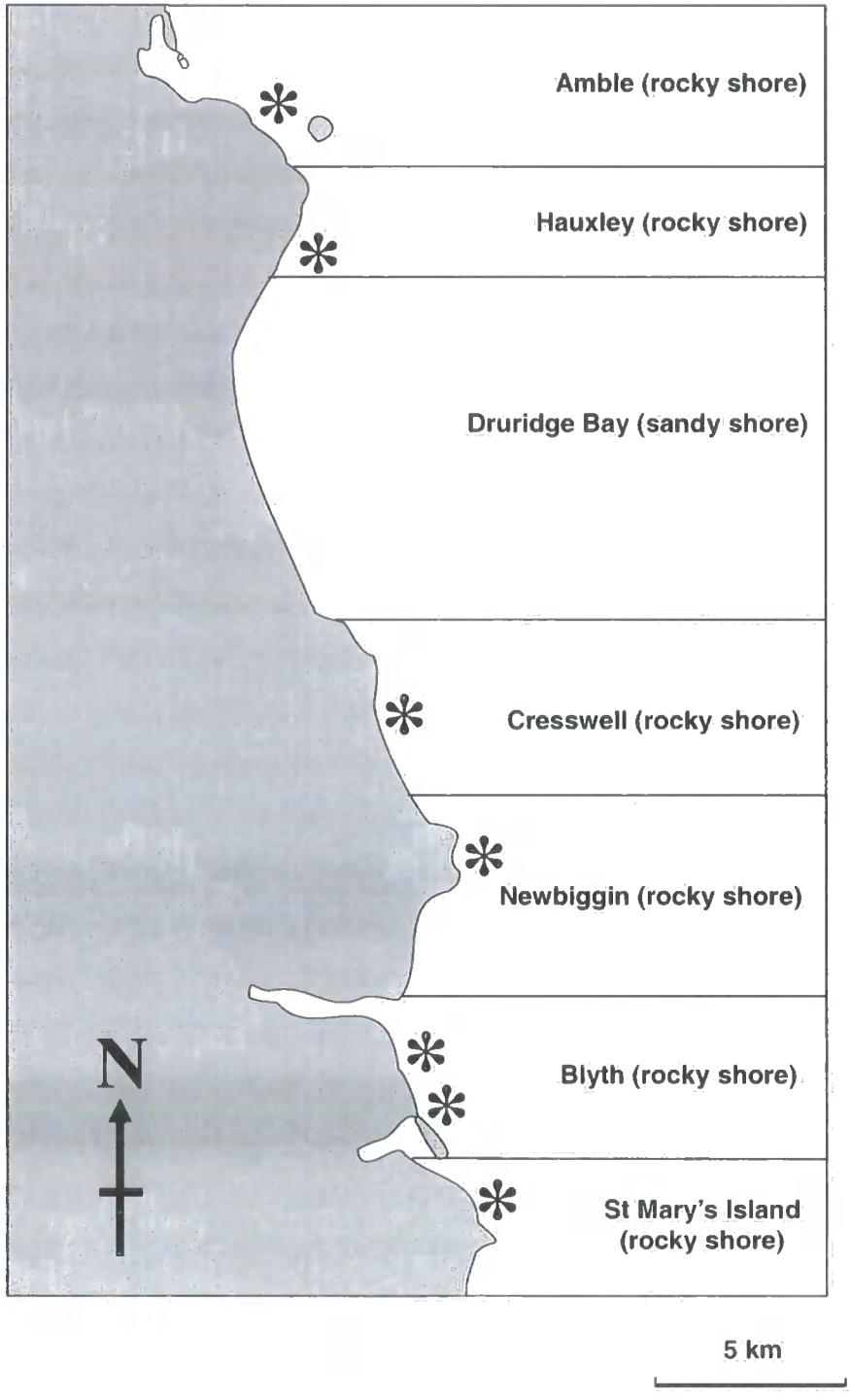
1.1.1 Physical features

The study area comprises the coastal zone of southern Northumberland (north-east England) between Warkworth Harbour (55º 20' 25"N 1º 35' 33"W) in the north and St. Mary's Island (55º 4' 37"N 1º 27' 8"W) in the south (see figure 1.1). It is a complex, but broadly linear coastline, with a mix of rocky shore backing onto dunes or low cliffs (typically about four metres in height), and sandy beaches of varying length. A shallow offshore dip promotes the exposure of flat platforms, topographical features associated with high densities of rocky shore specialist shorebirds, in particular ruddy turnstones

[1] The term wrack is often used to refer to marine algae of the genus *Fucus*. It is here used in the wider sense of marine vegetation, algae or the like, cast ashore by wave action.

and purple sandpipers *Calidris maritima* (Brunnich) (Anthony 1999). Primary divisions of the study area were based on habitat discontinuities and are summarised in figure 1.1. See Eaton (2001) for further information on the study area.

Figure 1.1 Map of the study area with locations of sewage outfalls (denoted by an asterisk), site names and principal habitat divisions. Land is shaded grey.



A southerly surface current occurs off the Northumberland coast between Tynemouth and Newbiggin-by-the-sea, although there is no prevailing current at deeper levels (Evans 1957, 1959). Within each tidal cycle, an elliptical stream occurs, rotating clockwise on the surface, and anti-clockwise near the bottom, where the stream turns onshore at low water. This means that beach casting of suspended and floating marine debris is most likely to occur at the end of the ebb period, about 2.5 hours after low water (Evans 1959).

1.1.2 Habitats

Ruddy turnstones use a wide variety of habitats, both soft-sediment and rocky substrates, although the latter is preferred, particularly by wintering birds (Cramp & Simmons 1983). Indeed, of the intertidal habitats, rocky shore is used almost exclusively by ruddy turnstones in the present study area (Eaton 2001). Rocky shore habitats within the study area comprise bare wave-cut platforms colonised by small barnacles and mussels, as well as areas dominated by the growth of macroalgae, principally *Fucus* spp, *Enteromorpha* spp and *Ascophyllum nodosum* (L.). For the purposes of this study, two contrasting intertidal habitats were selected for data collection: *Fucus*-covered rocks and barnacle-covered rocks. These were the most abundant habitats, and those present most evenly in rocky intertidal areas throughout the length of the study site. Furthermore, birds foraging on barnacle-covered rocks may be more visible to predators than birds using *Fucus*-covered rocks (Metcalfe 1984), presenting a natural experiment with which to look for responses to variation in predation risk.

Supratidal habitats used by shorebirds in the study area included deposits of beach-cast wrack and strandline debris, fields, golf courses, piers, staiths, and other artificial structures. Artificial supratidal habitats were used relatively rarely by ruddy turnstones, so the two main types of natural supratidal habitats were distinguished for data collection. These were beach-cast wrack, and strandline sand or algal material.

Beach-cast wrack deposits, here defined as discrete aggregations of marine vegetation, algae and the like, cast ashore by wave action, occurred throughout the study site and were strongly selected by ruddy turnstones (see chapter 3). My definition of beach-cast wrack is equivalent to the wrack beds of Backlund (1945) and Egglishaw (1960). See chapter 3 for detailed information on beach-cast wrack.

The other main supratidal foraging habitat for ruddy turnstones was close to the surf on sand more or less obviously strewn with strandline debris. Some strandline deposits were formed as beach-cast wrack was resuspended by wave action. This tended to result in damp algal material containing dead coelopid wrack flies that had colonised the beach-cast wrack, whereas naturally deposited strandline debris ("wrack strings" of Backlund 1945) tended to be loose, dry material colonised by amphipods and occasionally Coleoptera (Egglishaw 1965). Beach-cast wrack tended to occur close to the base of the cliff backing the beach, whereas strandline debris occurred much further from the cliff base, near the high water mark (see figure 3.1 on page 41 for a diagram of a typical beach-cast wrack deposit).

1.1.3 Anthropogenic influences

In February 2000, the Northumbria Coast was declared a Ramsar Site and a Special Protection Area (SPA), with most rocky shore areas falling within the designation. This was based on a study of spatial distributions of ruddy turnstones and purple sandpipers, both species of some European conservation concern (Anthony 1999). Most stretches of sandy shore were specifically excluded from this designation, despite the fact that beach-cast wrack often forms on sandy substrates. The Northumbria Coast Ramsar Site supports 2.5% and 1.5% of Europe's wintering ruddy turnstones and purple sandpipers respectively (Anthony 1999) and it is a requirement of European law (EEC 1979) that significant pollution, disturbance, and deterioration of an SPA are avoided.

As a result of European and national legislation, water companies in the UK have invested heavily in new and improved coastal sewage treatment plants (EEC 1991). This fact, coupled with the banning of the dumping of sewage sludge at sea, suggests that levels of nutrients and sewage-derived suspended solids in the coastal zone will continue to fall over the coming years, despite the relatively low level of nutrient enrichment currently apparent in the western North Sea (Reid 1995). This could potentially impact foraging shorebirds through reductions in intertidal food availability or even reduce the carrying capacity of the nearshore environment. During summer 2001, Northumbrian Water, the company responsible for water supply and sewage treatment in the present study area, upgraded the level of treatment given to sewage before discharge into the North Sea to at least secondary treatment (Northumbrian Water Limited 2001). This followed an earlier wave of improvements, completed in 1999, during which interceptor sewers were installed to concentrate output at fewer, more carefully selected sites. Seven offshore sewage outfalls have been built within the boundaries of the study area (see table 1.1). The present research programme focuses on foraging decisions made by ruddy turnstones, and the results are discussed in chapter 7 in the light of possible changes in allochthonous nutrient input into the nearshore ecosystem.

Table 1.1 Former and current sewage outflow sites within the study area. Interceptor sewers at Cresswell and St Mary's Island now pump sewage to other treatment works for disposal, so there has been a complete cessation of effluent dumping at these sites (Northumbrian Water Limited 2001). See figure 1.1 for locations of the sewage outfalls.

Site	Status
Amble	Secondary treatment output through an outfall
Hauxley	Secondary treatment output through an outfall
Cresswell	Interceptor sewer now in place
Newbiggin	Secondary treatment output through an outfall
Blyth (north)	Secondary treatment output through an outfall
Blyth (south)	Secondary treatment output through an outfall
St Mary's Island	Interceptor sewer now in place

There is a large literature on the effects of organic pollution on benthic, planktonic, and nektonic organisms (see Pearson & Rosenberg 1978, Welch 1992 and Green et al. 1993 for reviews). Much of the evidence is correlational in nature, and although the theory of many interactions is becoming advanced, demonstrations of causal pathways remain limited. Shorebirds forage widely over the intertidal zone and are likely to integrate a wide span of spatial and temporal information on habitat quality (Furness et al. 1993), and as occupiers of high positions in the food web, can act as bioindicators of general "ecosystem health" (McKenzie et al. 1992).

It has been suggested that changes in the frequency that shorebirds feed supratidally may reflect changes in intertidal habitat quality (Smart & Gill 2003). This suggestion rests on a number of as yet untested assumptions about the causal basis of supratidal feeding. Before we can use supratidal feeding as an index of habitat quality, we need to establish whether the basis for supratidal feeding is similar across different shorebird foraging systems.

1.1.4 Study species

The ruddy turnstone is a coastal species, breeding along the northernmost fringes of the Holarctic, and spending the non-breeding season around mid to low latitude coasts in the northern and southern hemispheres. One of the most northerly breeding waders, its distribution is more or less circumpolar, and two subspecies are recognised. The nominate *interpres* breeds from the eastern Canadian Arctic across Greenland and northern Eurasia to western and northern Alaska, while *morinella* breeds in arctic Canada west of Ellesmere Island (Cramp & Simmons 1983). Breeding birds occur up to 83º N in Greenland and 80º N in Svalbard, and as far south as the southern Baltic Sea. The ruddy turnstone is apparently declining in the Baltic, but little is known of population trends in arctic regions (Hagemeijer & Blair 1997).

Most birds wintering in north-east England are from the Greenland and eastern Canadian Arctic populations. These birds can be identified in autumn by having commenced wing moult and showing no significant fat reserve with

which to continue onward migration (Branson et al. 1978). Birds thought to be of Fenno-Scandian origin (Prater 1981) on autumn passage through Britain are heavier, with fat reserves for onward migration to Africa, and have not yet commenced wing moult. These latter birds put on weight rapidly during their staging in Britain and then depart (Clapham 1979).

Ruddy turnstones winter along virtually all coastline of the British Isles (Prater 1981), although the poor coverage of non-estuarine coast by national surveys makes it difficult to generate a complete winter population estimate. The maximum UK winter population was estimated at 25,000 (Prater 1981), although this estimate involved extrapolation from survey work concentrated mainly on estuaries, and included anecdotal data from county bird reports and other sources. This may be a substantial underestimate if the proportion of birds using non-estuarine habitats is as high as the figure of 80% suggested by Waters & Cranswick (1993).

The basic social foraging unit in wintering ruddy turnstones is a group of c. 20 - 80 birds sharing a stable intertidal area, with a strongly linear dominance hierarchy (Metcalfe & Furness 1985, Metcalfe 1986). Winter flocking in many shorebirds is probably associated with decreased predation risk, rather than enhanced feeding success (Page & Whitacre 1975, Whitfield 1988a). Most individual ruddy turnstones are site faithful within and between winters, although some are more itinerant, probably as a result of instability in their food supply (Metcalfe & Furness 1985, Whitfield 1988a). Dominance is of males over females, adults over juveniles, and within a sex, older birds over younger birds. Rank decays with distance from an individual's home low tide feeding group (Whitfield 1985a, Metcalfe 1986, Whitfield 1988b). Variable plumage features during winter facilitate individual recognition rather than status signalling, as is predicted in a species showing stable group membership and extreme site fidelity (Whitfield 1988b).

The ruddy turnstone is particularly well suited to a study of this kind, because in rocky shore habitats it is thought to be largely limited to diurnal foraging (Evans 1976). Many shorebirds possess a concentration of bill-tip Herbst

corpuscles used for tactile foraging either to locate hidden prey or forage at night (Gerritsen and Meiboom 1986, Piersma et al. 1998, Barbosa & Moreno 1999), but the ruddy turnstone possesses few of these mechanoreceptors (Hoerschelmann 1972) and thus may be restricted largely to a visual foraging mode. Despite some evidence of nocturnal foraging by ruddy turnstones and other shorebirds in soft-sediment habitats (Clark et al. 1990, Robert et al. 1989, Schneider 1985), it appears likely that ruddy turnstones rarely forage at night on rocky shores, confirmed at least for the present study population by recent radio-telemetry studies (Eaton 2001). Responses to variation in food availability in this species are therefore likely to be marked owing to its reduced maximum possible daily foraging time in comparison with other members of the species assemblage.

1.2 Research questions

1.2.1 Does the quality of alternative foraging substrates predict the frequency of their use?

An important factor influencing the choice of foraging area is the relative quality of alternative possible foraging substrates in terms of potential energy intake rate (Stephens & Krebs 1986, Zwarts et al. 1996). I therefore first set out (chapter 2) to quantify prey densities and energy intake rates on the four main ruddy turnstone foraging habitats identified in section 1.1.2. The density of potential prey items did not differ between intertidal and supratidal habitats, although the energy intake rate per unit time was much higher for foragers using supratidal habitats. This finding was not unexpected, but threw up interesting questions that influenced the direction of the study. Supratidal habitats were always available to ruddy turnstones, and they appeared to be more profitable in terms of potential energy intake rate than intertidal habitats. Why then did foragers concentrate exclusively on intertidal habitats when these were available during low water, ignoring supratidal habitats? What was driving the decision to feed supratidally, and were there costs associated with feeding so high up the shore?

1.2.2 What are the spatial and temporal dynamics of supratidal foraging substrates?

To help answer these questions about the apparent reluctance of shorebirds to use a profitable habitat, I needed to understand what was driving the decision to feed supratidally by describing the relationship between supratidal habitat availability and foraging decisions made by birds. There is little published information on the dynamics of supratidal habitats (Kirkman & Kendrick 1997), so chapter 3 describes the variation in spatial extent, quality, and temporal predictability of beach-cast wrack, the principal supratidal habitat used by ruddy turnstones. The chapter describes the physical and decompositional characteristics of deposits associated with large invertebrate colonisation events and discusses whether the future quality of a deposit is predictable by foragers, or at least exhibits temporal autocorrelation. The results showed that beach-cast wrack occurred in low predictability patches in an otherwise highly stable matrix of intertidal habitats. The emerging theme of the research project became trying to understand what was limiting the extent to which individuals exploited this unpredictable habitat and the implications for foraging theory.

1.2.3 Are there differences in perceived predation risk and foraging behaviour between intertidal and supratidal habitats?

One potential cost of foraging high up the shore that might limit supratidal feeding is elevated predation risk (Whitfield 1985b). Therefore, I next examined the level of predation risk perceived by foragers on alternative possible foraging substrates. If predation risk differed among the habitats, I predicted vigilance levels to be adjusted above that predicted by flock size alone on high risk habitats, and below that predicted by flock size alone on low risk habitats. I tested these predictions using comparisons between intertidal and supratidal habitats and alternative substrates thought to differ in predation risk within each of these broad habitat types. Chapter 4 shows that vigilance levels were adjusted as predicted, and also uncovers diurnal patterns in vigilance and intake rate consistent with the predictions of state-

dependent foraging theory on substrates varying in predation risk and resource dynamics. My data supported the suggestion that elevated predation risk was a cost of foraging supratidally in this system.

1.2.4 Do foragers try to avoid the need to feed supratidally by ranging more widely?

Given that elevated predation risk appeared to be at least one cost associated with supratidal feeding, I next examined the relationship between spatial ranging behaviour of ruddy turnstones and their individual propensity to feed supratidally. Most ruddy turnstones are exceptionally site faithful, and dominance rank appears to decline with distance from the centre of an individual's home range (Metcalfe 1986). This suggests a social cost to ranging widely, but if feeding supratidally carries a cost of increased predation risk, a forager might be prepared to range more widely on intertidal habitats to track areas of high profitability thereby minimising the need to forage supratidally. For example, a highly site-faithful forager may have to accept more risk through environmental stochasticity than a forager that ranges more widely.

In chapter 5, I show that birds that ranged more widely also tended to feed less frequently on supratidal habitats. Furthermore, birds that frequently fed supratidally were more closely associated with reliable areas for the formation of beach-cast wrack deposits than birds that fed supratidally less frequently. Several independent lines of evidence now suggested that supratidal feeding carried a cost, most likely predation risk, and that foragers compensated for this by altering their spatial distribution, as well as their antipredator responses.

1.2.5 What drives the decision to feed supratidally?

After I had painted a picture of resource dynamics, foraging behaviour, vigilance adjustment and spatial associations, it remained to pull these elements together and look for convincing evidence of what was driving the decision to feed supratidally. If variation in energy intake while foraging intertidally was driving supratidal foraging, we would predict the proportion of the population feeding supratidally to be independent of the quality of supratidal foraging patches. In chapter 6, I therefore wanted to know (a) whether birds were more likely to feed supratidally when the availability of supratidal habitats was higher and (b) something about the individual characteristics (e.g. age, sex, rank) of persistent supratidal feeders. The data supported the explanation that variation in intertidal energy intake was driving the decision to feed supratidally, and indeed most supratidal feeding occurred over the high water period. Furthermore, higher ranking birds tended to feed supratidally more frequently than lower ranking birds.

I distinguish four hypotheses that could explain the observed distribution of foragers, and conclude that all data collected during the course of this work suggest that supratidal feeding is a form of "reluctant compensation", whereby some foragers pay for their extreme site fidelity by feeding more frequently on risky habitats, thereby accepting elevated predation risk at particular points during their foraging cycle.

Chapter 2: The energetic quality of alternative ruddy turnstone foraging substrates

2.1 Introduction

Understanding the reasons why animals choose one place to forage over another has been the focus of a substantial body of research over many years (MacArthur & Pianka 1966, Morse & Fritz 1982, Milinski 1985, Brown 1988, Mangel & Clark 1988, Johnson & Collier 1989, Wilmshurst et al. 1995). Probably the single most important parameter influencing this decision is the relative quality of alternative foraging patches, namely the density and net energetic value to the consumer of potential prey items inhabiting different possible foraging areas (Stephens & Krebs 1986, Zwarts et al. 1996, Schmidt et al. 1998, Wajnberg et al. 2000, Olsson et al. 2001). Typically, the number of foragers at a patch will be proportional to the quality of that patch (Fretwell & Lucas 1970). Although this distribution is influenced by many other factors, such as predation risk (Brown 1988), competitive ability (Parker & Sutherland 1986) and interference (Meer & Ens 1997), it remains the best approximation to many distributions of foragers under natural conditions.

Possible foraging habitats of many species vary greatly in the taxonomic and numeric composition of potential prey types, as well as their energy values, digestibility, and handling times (Palmer 1981). For example, ruddy turnstones have been recorded foraging on many different substrates, and are well known for their opportunism (Bayne 1941, Hobbs 1942, Bell 1961, King 1961, MacDonald & Parmalee 1962, Selway & Kendall 1965, Mercer 1966, Jones 1975, Beven & England 1977, Nettleship 1973, Cramp & Simmons 1983, Whitfield 1990, Dobson 1997, Eaton 2001). There is, however, very little information about the relative quality of the most frequently used alternative substrates in terms of density and profitability of available food. Ruddy turnstones are known to take different food items in different habitats, but are relatively conservative within a given habitat. On rocky intertidal areas around Morecambe Bay, NW England, they chiefly took

amphipods and small littorinids, but also barnacles, small *Mytilus*, and crabs (Davidson 1971, Prater 1972). In similar habitat in Anglesey, north Wales, they again took mainly amphipods, littorinids and barnacles (Harris 1979). Analyses of pellets and stomach contents of German and Dutch birds using intertidal rocky shore habitats also indicated a reliance on crustaceans, in particular amphipods and barnacles (Glutz von Blotzheim et al. 1977). In contrast, in soft-sediment habitats such as the Wash, south-east England, ruddy turnstones concentrated on crabs and molluscan infauna (Jones 1975). Ruddy turnstones appear then to consume relatively few different prey types while foraging intertidally, at least on rocky shore substrates.

Little published information exists on the diet of ruddy turnstones while foraging on supratidal habitats, although they appear to use a much greater variety of habitats while foraging supratidally than intertidally (Cramp & Simmons 1983). The present study has shown that beach-cast wrack is the preferred supratidal foraging habitat on the Northumberland coast (see chapter 3), and Eaton (2001) suggested that ruddy turnstones rely mainly on larval coelopid wrack flies while using this habitat. Coelopids are indeed the main colonisers of beach-cast wrack in NE England (chapter 3; Egglishaw 1965).

The superabundance of coelopids in beach-cast wrack deposits suggests that, in the present study site at least, supratidal foraging may be more profitable in terms of energy intake per unit time than intertidal foraging. Nevertheless, many shorebird species, including ruddy turnstones, use intertidal habitats almost exclusively when these are available, and usually use supratidal habitats only over the high water period, when intertidal habitats are unavailable (Fleischer 1983, Goss-Custard et al. 1996, Dann 1999, Masero & Perez-Hurtado 2001, Smart & Gill 2003, but see Luis et al. 2002). Indeed, within the present study systems, ruddy turnstones prefer to use intertidal habitats when these are available (Eaton 2001). This reluctance to use supratidal habitats is perplexing, given that supratidal habitats are apparently highly profitable relative to intertidal habitats.

There are two broad classes of explanation for this apparent reluctance to feed supratidally. Either intertidal habitats are in fact richer than supratidal habitats, perhaps by high invertebrate densities compensating for their low individual calorific value, or there is some cost incurred by foraging supratidally that is sometimes worth paying when the opportunity of feeding intertidally is not available. To discriminate between these possibilities, it is crucial to obtain comparative data on instantaneous energy intake rate for the alternative habitats (Masero 2003). If potential energy intake rate is greater on supratidal than intertidal habitats, we might indeed expect there to be some cost of feeding supratidally. This chapter therefore provides new information on the relative profitabilities of alternative ruddy turnstone foraging substrates for an area of natural, predominantly rocky coastline in north-east England.

As well as information about the energy content and relative density of available potential prey items, an understanding of the profitability of a foraging substrate requires information on the energetic requirements of the forager (Pienkowski et al. 1984). Shorebirds breeding at high latitudes and undergoing long migrations typically have a higher basal metabolic rate (BMR) and daily energy expenditure (DEE) than predicted by their body size (Kendeigh 1970, King 1974, Kersten & Piersma 1987). A high BMR may enable birds to ratchet up their DEE to a level necessary for coping with extreme energy demand, for example through thermal stress while wintering in northern latitudes, and during periods of high muscular activity while migrating (Gnaiger 1987, Kersten & Piersma 1987). However, the relationship between BMR and DEE is less clear in birds than in mammals (Koteja 1991, Ricklefs et al. 1996, Nagy et al. 1999). For example, evidence is emerging that individual birds may facultatively alter the percentage composition of metabolically active tissues to achieve a high maximal metabolic rate when necessary (Daan et al. 1990, Piersma et al. 1995,1996, but see Selman 1998). Whatever the mechanisms involved, the high DEE associated with shorebirds implies strong evolutionary pressure for foragers to select the most profitable foraging substrates. This is particularly important for populations of ruddy turnstones wintering in short daylengths at high

latitudes, because this species feeds visually and is largely restricted to diurnal foraging in rocky intertidal areas (Hoerschelmann 1972, Eaton 2001).

Using the regression equation in Kersten & Piersma (1987), existence metabolism for ruddy turnstones experiencing an average daily temperature of 6.6 ºC as in this study should be about 250 kJ per day (-3.9 * 6.6 + 277). Net energy intake (NEI) will be substantially higher than this figure, and a value of 300 kJ per day is probably more representative of the NEI of free-living ruddy turnstones, given that ringed plovers *Charadrius hiaticula* L. (a slightly smaller bird) in north-east England took 159 - 192 kJ per day and grey plovers *Pluvialis squatarola* (L.) (slightly larger bird) took 309 - 392 kJ per day (Pienkowski 1982). Given that the NEI values quoted here were recalculated assuming an assimilation efficiency of 85% (see Evans et al. 1979), a value of about 350 kJ per day seems a reasonable estimate of gross daily energy requirement. Further support for this value comes from the fact that incubating ruddy turnstones had a field metabolic rate of 348.1 kJ per day (Piersma & Morrison 1994, Morrison et al. 1997, Piersma et al. 2003). Although red knot *Calidris canutus* (L.) wintering in Africa showed reduced metabolic activity (Lindström 1997, Kersten et al. 1998), birds wintering in temperate latitudes showed a similar DEE as when on their arctic breeding grounds (Piersma 2002).

Some supratidal foraging habitats, beach-cast wrack in particular (see chapter 3), contain very high densities of potential prey items, but they can also be temporally unstable. Here I test the hypothesis that supratidal habitats (strandline debris and beach-cast wrack) are richer in terms of potential energy intake than intertidal habitats (*Fucus*-covered rocks, barnacle-covered rocks). I then relate the energetic values of potential prey items found in the alternative substrates to the estimated energy requirements of free-living ruddy turnstones.

2.2 Methods

2.2.1 Intertidal habitats

Intertidal habitats were represented by *Fucus*-covered rocks and barnacle-covered rocks. *Fucus*-covered rock was defined as bedrock with a complete overgrowth of *Fucus serratus* L. or *F. vesiculosus* L. Barnacle-covered rock was defined as bedrock with complete or near-complete overgrowth with *Semibalanus balanoides* (L.), and no algal growth. Transects in both habitats were run for 300 m up the shore from the low tide mark (1.1 m above chart datum) during a spring tide series in early March 2003 at Amble, NE England (55º 20' 09"N 1º 33' 58"W). Random number tables were used to select co-ordinates within each 10 * 10 m grid along the transect, resulting in 30 sampling locations. A 10 * 10 cm quadrat was placed on the substrate at each randomly defined location, and all material transferred as quickly as possible into a sealed container.

In the case of *Fucus*-covered rocks, 30 samples were taken, and scissors were used to cut the algae using the quadrat as a guide, aiming to cause minimal disturbance to mobile invertebrates within the algae. Amphipods seen in the field all appeared to move rather slowly along algal fronds upon being exposed, and generally stayed in close contact with the algal substrate at all times. Once all the algae had been transferred into the container, the exposed substrate below was checked carefully for remaining mobile invertebrates, which were also transferred into the sealed container. Sessile organisms on the rock surface were identified to genus level and the numbers of each taxon recorded.

Because barnacle-covered rock was a relatively rare habitat, the nearest patch of barnacle-covered rock to 10 randomly-defined co-ordinate locations was used. The number of barnacles within the quadrat was counted, and a careful search was made for empty barnacle cases that had been colonised e.g. by gastropod molluscs or mussels *Mytilus edulis*. Invertebrates

colonising empty barnacle cases were counted, removed and stored separately by species. All barnacles within each quadrat were then scraped off the substrate with a knife and transferred into a sealed container.

2.2.2 Supratidal habitats

Supratidal habitats were represented by beach-cast wrack and strandline. In the case of beach-cast wrack, the samples taken from two wrack deposits at Cresswell (55º 13' 44"N 1º 31' 41"W) and one at St Mary's Island (55º 4' 14"N 1º 27' 10"W) were used (see chapter 3 for detailed methods). Samples were obtained by placing a 10 cm * 10 cm quadrat on the surface of the beach-cast wrack deposit, and cutting a litre cube out of the material, using the quadrat as a guide. Sixty-six samples were removed from the wrack deposit and transferred to sealed containers as quickly as possible to minimise escape by invertebrates.

Strandline invertebrates were sampled in a similar way by transferring 20 one-litre samples of strand material, including the sandy substrate underneath where the strand material was less than 10 cm in depth, to sealed containers as quickly as possible. Sampling was carried out at South Amble on 28th November 2001 and 11th January 2002. The first set of samples was taken from loose, dry strandline debris and the other from strandline comprising previously beach-cast material in the process of resuspension. This reflected the two major types of strandline habitat used by ruddy turnstones in this study (see chapter 1).

The sampling regime on the two habitat types was designed to sample the density of prey available to foragers within a specific area (1 dm^2). In intertidal habitats, this meant scraping algal material from rocks to whatever depth it grew down to the rock surface. In supratidal habitats, samples were taken to a depth of 10 cm into the substrate, because observations of foraging birds suggested this was the maximum depth they could reach by excavating holes in the substrate. Therefore, although the precise volume of material sampled was different in intertidal versus supratidal habitats, both

sets of samples represented the density of available potential prey within a given area of foraging substrate.

2.2.3 Estimating the energy content of prey species

Samples were washed thoroughly over a 1 mm sieve and all macroinvertebrates were separated from algae or other material, identified to genus level, counted and removed. They were then killed by rapid freezing and stored in a dry sealed container. Invertebrates were washed in distilled water and any remaining surface water was blotted into tissue paper. At this stage, the invertebrates were divided into single species samples for calorimetry. Samples of each species were freeze-dried to constant weight, homogenised thoroughly, and combusted in a Gallenkamp bomb calorimeter. The change in temperature of the shell of the calorimeter was calibrated against the change observed when known weights of benzoic acid were combusted. A regression model was fitted to the relationship between the initial dry weight of three benzoic acid samples and the temperature achieved by the calorimeter shell (TEMP = 116.3 * WEIGHT - 2.24, $R^2 = 0.99$, d.f. = 2, $p = 0.024$). The benzoic acid had a known calorific value of 26.454 kJ g^{-1}, thus the energy content of each sample could be estimated using the regression relationship. The amount of material left after combustion was weighed to provide a measure of indigestible content in the prey items. The proportion of organic material was calculated by dividing ash weight into the dry weight for each sample, and the water content by dividing dry weight into wet weight for each sample.

2.2.4 Ruddy turnstone energy requirements and meal intake rates

As discussed earlier, an approximate DEE of 350 kJ was used to estimate ruddy turnstone energy requirements. Average meal intake rates by ruddy turnstones foraging on the four substrates were taken from chapter 4. Birds were observed for 5-minute periods while foraging intertidally and supratidally to ascertain the proportion of time in each habitat that they spent feeding as opposed to roosting or performing maintenance or vigilance behaviours (see

chapter 4 for detailed methods). Of the time that birds were observed in the two habitats, they spent 0.78 (n = 16, range: 0.70 – 0.88) of their time actively searching for food in intertidal habitats and 0.87 (n = 20, range: 0.79 – 0.98) of their time actively searching for food in supratidal habitats. Because there appeared to be substantial individual variation in the proportion of time birds spent foraging, NEI values were calculated using mean, minimum and maximum values for time spent actively foraging.

2.3 Results

2.3.1 Potential prey types

Five main groups of potential prey types were found across the four habitats: amphipods, gastropod molluscs of the genus *Littorina*, bivalve molluscs of the genus *Mytilus*, barnacles of the genus *Semibalanus*, and wrack fly larvae of the genus *Coelopa* (table 2.1).

Table 2.1 Numbers of individuals of the main invertebrate groups present in different habitats. For intertidal habitats (*Fucus*- and barnacle-covered rocks), invertebrates were scraped from the surface; for supratidal habitats (strandline and beach-cast wrack), invertebrates were sampled from the top 10 cm of the substrate. Values are numbers of individuals per sample ± 1 SD. N signifies the number of samples taken (dm^2 quadrats in the case of intertidal habitats, and litre samples in the case of supratidal habitats).

Habitat	N	Amphipods	Littorinids	*Mytilus*	Barnacles	Coelopids
INTERTIDAL						
Fucus-covered rocks	30	4.2 ± 4.59	2.2 ± 6.5	1.0 ± 4.0	41.3 ± 53.1	0
Barnacle-covered rocks	10	0	4.4 ± 3.1	3.9 ± 2.1	265 ± 115.5	0
SUPRATIDAL						
Strandline	20	5.5 ± 3.5	0	0	0	14.9 ± 30.1
Beach-cast wrack	66	0.045 ± 0.21	0	0	0	442.2 ± 684.6

2.3.2 Intertidal habitats

Intertidal habitats contained low densities of littorinids, *Mytilus*, and amphipods, but very high densities of barnacles in suitable open habitat. Open barnacle-covered rocks also tended to support higher densities of littorinids and *Mytilus* than *Fucus*-covered rocks, many of which inhabited empty barnacle cases, presumably for shelter. Littorinids generally occurred at slightly higher densities than *Mytilus* in both habitats and all animals in intertidal habitats were less than 5 mm in length. Amphipods were found only on *Fucus*-covered rocks, where they were closely associated with damp algal fronds. With the exception of barnacles, all invertebrates on intertidal habitats occurred at densities of less than 5 individuals per dm^2 (table 2.1). Barnacles, however, were superabundant in suitable habitat patches, with a mean density of 265 individuals per dm^2, and achieving a maximum density of 400 individuals per dm^2. There was a weak trend for decreasing invertebrate density with increasing distance from the low tide mark, but this was not statistically significant ($r = 0.28$, $n = 30$, $p = 0.128$), suggesting that intertidal habitat quality did not vary greatly with the height of the tide.

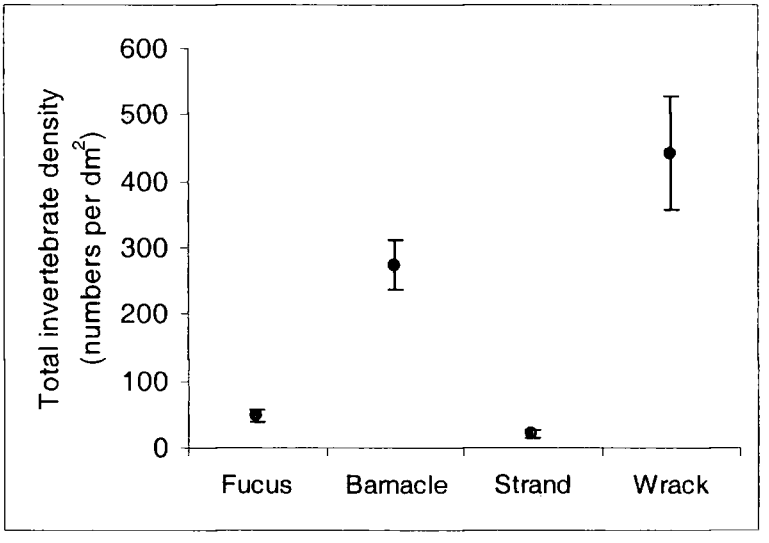
2.3.3 Supratidal habitats

The taxonomic composition of the samples from intertidal and supratidal habitats was very different. Coelopid flies occurred in both supratidal habitats, although at a much higher mean density in beach-cast wrack (442 individuals l^{-1}) than in strandline debris (15 individuals l^{-1}). Strandline debris only held coelopids where it was formed by beach-cast wrack material undergoing resuspension, and many of the flies were dead or dying. Amphipods also occurred in both supratidal habitats, but at a higher mean density in strandline debris (6 individuals l^{-1}) than beach-cast wrack (0.05 individuals l^{-1}).

2.3.4 Comparison of invertebrate faunas among the substrates

The overall density of potential invertebrate prey species varied significantly among the four sampled substrates (one way ANOVA: $F_{3,122} = 12.07$, $p < 0.001$), but was similar on intertidal and supratidal habitats ($t = 0.69$, d.f. = 108.5, $p = 0.422$). The differences in invertebrate densities among substrates were driven by high densities on barnacle-covered rock and beach-cast wrack and low densities on strandline debris and *Fucus*-covered rock (see figure 2.1).

Figure 2.1 *Fucus*-covered rocks and strandline debris contained significantly fewer invertebrates than barnacle-covered rocks and beach-cast wrack (Tukey post-hoc tests: all $p < 0.01$). The high densities in barnacle-covered rocks and beach-cast wrack were generated by barnacles and coelopids respectively. Error bars are ± 1 SE. Because of the different nature of the two habitat types, macroinvertebrate densities were measured in 10 * 10 cm quadrats in the case of intertidal habitats and litre samples in the case of supratidal habitats. Although collected using different sampling techniques, these two measures approximate to the density of prey available to foragers in a 10 * 10 cm surface area of foraging substrate (see text for details).



2.3.5 Energy value of prey species

The oligochaetes found on *Fucus*-covered rocks were excluded from calculations of energetic values, as they were extremely small and unlikely to be detectable in the field by ruddy turnstones, which forage visually. Moreover, their exclusion from further analysis could only lead to an overestimation of average energy value of intertidal prey items; this was therefore a conservative approach.

Energy value and organic content of the different potential prey types varied widely (table 2.2). Coelopid larvae had by far the highest energy content (0.147 kJ per individual), and also a very low ash content (9%). All other prey types had much lower values for energy content, between 0.044 kJ per individual (amphipods) and 0.072 kJ per individual (littorinids). The three shelled prey types (littorinids, *Mytilus* and barnacles) contained a very high proportion of ash (63 - 87%) and a low proportion of water (33 - 54%). This reflects the high proportion of indigestible hard body parts in these animals. The small size of amphipods appeared to be responsible for their relatively low energy value per individual, because their energy value per g of dry weight was relatively high (15.15 kJ g^{-1}).

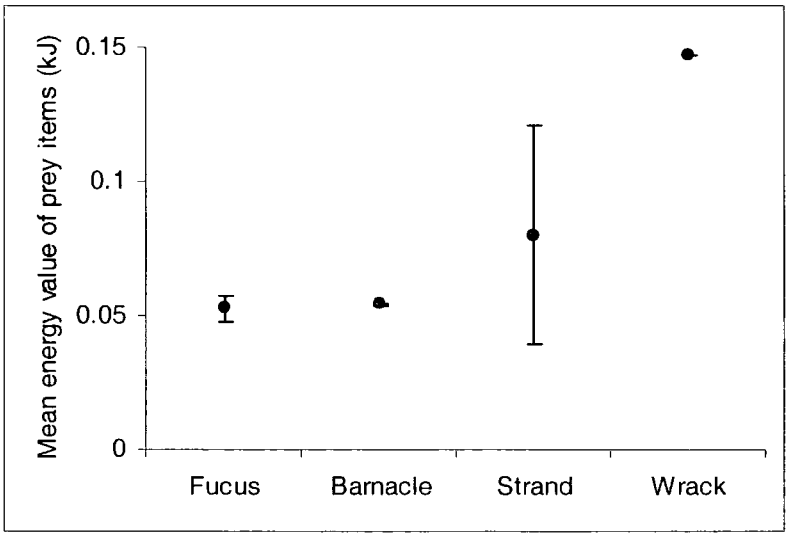
Table 2.2 Energy value and ash content of potential prey types inhabiting alternative ruddy turnstone foraging substrates. Where more than one sample was obtained of a prey type, values are averaged. N represents the number of samples analysed with the calorimeter.

Prey type	N	No. of indivs	Dry weight (g)	Water content (%)	Ash content by dry wt (%)	kJ/dry g	kJ/g AFDM	Energy per indiv. (kJ)
Amphipoda	2	138	0.40	77	24	15.15	19.94	0.0444
Littorinids	1	41	0.46	54	63	6.35	17.15	0.0718
Mytilus	1	31	0.32	44	72	4.97	17.75	0.0510
Barnacles	6	68	0.88	33	87	3.64	15.82	0.0540
Coelopids	5	192	1.07	79	9	29.48	32.39	0.1470

2.3.6 Energy value of alternative foraging substrates

To obtain an estimate of the energy value of an average potential prey item on each of the four substrates, the energy values of the different macroinvertebrate types were multiplied by their relative abundance in each of the samples (figure 2.2). The mean of these values were taken to represent the energy content of an average prey item in each sample for further analysis. Based on casual observations, the two strandline types (resuspending and dry) were estimated to occur with equal frequency. The energy value of an average potential prey item was much higher in supratidal than intertidal samples (Mann-Whitney test: $U_{80,40} = 333.0$, $p < 0.001$), and varied significantly among the substrates (Kruskall-Wallis test: $H = 102.3$, d.f. = 3, $p < 0.001$). The main source of variation in substrate profitability was the differing proportions of energy-rich coelopid flies among the substrates. The energy value of a typical prey item in strandline debris was much more variable than in other substrates. This was because some patches of strand comprised material from beach-cast wrack deposits undergoing resuspension, and therefore contained a relatively high proportion of coelopid wrack flies. Drier deposits of strandline debris contained only amphipods.

Figure 2.2 The energy value of an average potential prey item in each of the four main ruddy turnstone foraging substrates. Fucus = *Fucus*-covered rocks, Barnacle = barnacle-covered rocks, Strand = strandline debris, Wrack = beach-cast wrack. All comparisons were highly significant except that between the two intertidal habitats (Nemenyi post hoc tests: all $p < 0.01$; see Zar 1999). Error bars represent ± 1 SD.



2.3.7 Relative profitabilities in relation to energy requirements

Assuming a DEE of 350 kJ, an assimilation efficiency of 85%, and taking meal intake rates from chapter 4, table 2.3 gives the amount of time that, in the absence of selection, a ruddy turnstone would need to forage on each substrate to fulfil its daily energy requirement. The energetic value of an average prey item in each habitat was used to calculate the foraging time estimates. This approach assumed that foragers were indiscriminately ingesting all possible prey items found in the samples. To test the robustness of these results to possible selection of profitable prey items by foragers, table 2.4 gives the results assuming that birds fed only on the most energy rich prey items in each habitat. In accordance with initial expectations, ruddy turnstones foraging on supratidal habitats, particularly beach-cast wrack, should achieve their daily energy requirement much more quickly than birds foraging on intertidal habitats (table 2.3). This remained the case even when foragers were assumed to be highly selective (table 2.4). Mean daylength during the winter period (November - February) in the study area was 9.67 h. This means that on *Fucus*-covered rocks, a forager would need to spend 67% (or 49% if highly selective) of the daylight period foraging to achieve daily energy balance, assuming that rocky intertidal habitats were available throughout this time. Given that littorinids, the most profitable prey type on *Fucus*-covered rocks, occurred at very low densities (see table 2.1), it is unlikely that intertidal foragers could achieve a very high level of selection. However, regardless of selectivity, a forager would only have to spend 46% of the daylight period feeding on beach-cast wrack to achieve daily energy balance.

Table 2.3 Foraging time required to achieve daily energy balance assuming no selection by foragers, a DEE of 350 kJ per day (see text) using the mean, minimum and maximum values for the proportion of time birds spent foraging on each habitat type. Birds foraged on average for 0.78 of their time on intertidal habitats (range: 0.88 - 0.70) and 0.87 of their time on supratidal habitats (range: 0.79 - 0.98). Energy intake per minute was calculated using mean meal ingestion rates on the different substrates. The number of hours' foraging time required to reach daily energy target was then calculated assuming (a) birds foraged for the mean proportion of their time on each habitat, (b) the maximum observed proportion of their time and (c) the minimum observed proportion of their time.

	Fucus-covered rocks	Barnacle-covered rocks	Strand	Beach-cast wrack
Energy intake per minute (kJ)	0.9915	0.3113	0.5058	1.2934
Hours to reach daily energy target	6.47	20.59	11.36	4.44
Hours if foraged for minimum time	7.17	22.84	12.51	4.89
Hours if foraged for maximum time	5.75	18.31	10.09	3.94

Table 2.4 Foraging time required to achieve daily energy balance assuming that foragers always selected the most energy-rich prey items in each habitat (littorinids in intertidal habitats, coelopids in supratidal habitats). For strandline, I assumed that coelopids were available in 50% of the cases, and that foragers were forced to take amphipods in the other 50% of cases. See legend for table 2.3 for details of the calculations.

	Fucus-covered rocks	Barnacle-covered rocks	Strand	Beach-cast wrack
Energy intake per minute (kJ)	1.3518	0.4114	0.9272	1.2938
Hours to reach daily energy target	4.74	15.58	6.20	4.44
Hours if foraged for minimum time	5.26	17.29	6.83	4.89
Hours if foraged for maximum time	4.22	13.86	5.50	3.94

2.4 Discussion

2.4.1 Prey types and energy values for alternative foraging substrates

The five main prey types found in foraging habitats in this study accord well with what is currently known of the dietary preferences of ruddy turnstones. Previous studies on rocky intertidal systems have shown that amphipods, cirripeds, littorinids and *Mytilus* are the most frequent components of the diet of wintering ruddy turnstones (Davidson 1971, Prater 1972, Harris 1979). However, the relatively low energetic value of these prey types made intertidal habitats on average less profitable per meal obtained than supratidal habitats, where foragers concentrated on coelopid fly larvae and amphipods. The higher profitability of supratidal foraging substrates was not driven by a "superabundance" of prey items in supratidal habitats, as prey densities did not differ significantly between the two habitat types. Rather, the occurrence of energy-rich prey items in beach-cast wrack and strandline habitats was the key difference between intertidal and supratidal foraging profitabilities. Shorebird energy intake rates have recently been shown to be higher on supratidal salinas than on intertidal mudflats in Spain (Masero 2003). For the first time, this study provides information on a natural rocky shore system.

Intertidal habitats contained relatively few different potential prey types that also tended to have a low energetic value per individual. As the prey types found reflected closely those known to be taken by ruddy turnstones, we can be confident that the sampling protocol was providing a realistic picture of the available pool of prey. The results of the energetic analyses suggest that on intertidal habitats, amphipods were the most profitable prey item. Although the calorific value of individual amphipods was rather low because of their small size, their relatively low ash content (24%) implies that digestive efficiency would be higher than for the other prey types (mean ash content of non-amphipods = 72%). Ruddy turnstones always took small shelled organisms whole, so the inorganic content of their ingesta (e.g. calcite,

aragonite, nacre) would be very high relative to digestible material (Cummins & Wuycheck 1971). This would incur costs for intertidal foragers associated with the energy required to physically break down the hard parts in the gizzard, the time taken to achieve this, and the reduction in digestive efficiency because of the high proportion of inorganic material in the digestive system (Sibly & Calow 1986). These costs would be paid over and above the simple fact that the mean energy value per item consumed when foraging intertidally is lower than when foraging supratidally. Generalist species such as ruddy turnstones may show greater digestive plasticity than more specialist species (Hilton et al. 2000), for example by lengthening the gut. However, such physiological responses to a poor quality diet themselves carry costs in terms of manufacturing and maintaining those tissues (Sibly & Calow 1986).

Supratidal habitats also contained relatively few different potential prey types, but they had far higher energy value and lower ash content per individual. Coelopid flies had a high energy and water content, and also contained very little indigestible material. This suggests that both energy intake and digestive efficiency would be higher for birds foraging supratidally than for birds foraging intertidally. Further investigation of prey handling times, mechanical breakdown and digestibilities of alternative prey items is required to complete this picture, but this study has at least demonstrated a large differential in potential energy intake rates between intertidal and supratidal foraging habitats.

Very few identifiable hard parts have been found in the faeces of ruddy turnstones foraging supratidally (Eaton 2001). This makes intuitive sense, because coelopids contain very little indigestible cuticular and skeletal material, so little material will pass all the way through the digestive system. This reinforces the message that extreme care must be taken when interpreting results from analyses of faecal and stomach contents analysis, as digestion rates can vary dramatically and skew apparent proportions of prey types (Pienkowski et al. 1984, Votier et al. 2001, 2003). For example, redshanks are known to digest amphipods at a much faster rate than

Hydrobia (Goss-Custard 1969), the latter equivalent energetically to small littorinids in this study. The presence of soft-bodied prey items e.g. coelopids in the diet may therefore be completely overlooked using conventional dietary analyses of stomach, pellet or faecal contents.

Sampling of invertebrates during this study was carried out within a fairly small time window at the end of winter (early March), and it is possible that the quality of the potential prey items might change both within and between seasons. For example, intraspecific variation in the calorific value of lesser sandeels *Ammodytes marinus* Raitt is large enough to bias dietary studies using mean values (Hislop et al. 1991). Settlement of rocky shore invertebrates generally occurs in late spring, and growth occurs increasingly rapidly as temperatures increase through spring and summer (Lewis 1964, Pillay 1993). Growth slows dramatically or ceases during late autumn and winter. The intertidal invertebrate samples for this study were taken in early March, a time when any winter growth would have occurred, and no significant temperature-driven spring growth would have started. There is no evidence of seasonal variation in the size of coelopid larvae (Egglishaw 1960, Blanche 1992), and no obvious reason why this should occur in an insect with a very rapid life cycle inhabiting a seasonally uniform environment. The approach taken in this study is therefore conservative, in that intertidal invertebrates will be at their largest for the winter period. Further work extending these analyses across the entire winter period would, however, be interesting.

2.4.2 Time required to reach daily energy balance

The difference in profitability among the alternative foraging substrates led to a substantial inequality in the time required for a forager to achieve daily energy balance. This was approximately 4.5 hours in supratidal habitats and 6.5 hours in intertidal habitats. These values fit well with existing information on the length of time that ruddy turnstones spend feeding in a day (Eaton 2001). These values are conservative in that the analysis only considered the energy content of ingested prey items and applied a single estimate of

assimilation efficiency. It did not take account of additional costs and further reductions in digestive and assimilation efficiency caused by the high ash content of many intertidal invertebrates.

It has been shown experimentally that foragers can increase their energy intake rate under time constraints (Swennen et al. 1989, Lilliendahl et al. 1996), and it is possible here that ruddy turnstones could increase their intake rate facultatively under similar pressure, particularly on intertidal habitats. However, an increase in feeding rate in a field setting is likely to incur costs such as reduced time available for vigilance or maintenance behaviour, or greater risk of bill / muscle damage. Moreover, the low energy content of intertidal macroinvertebrates meant that even under conditions of extreme selection and foraging for a high proportion of its time, a forager would still do better on supratidal than intertidal habitats.

These analyses assume that handling time is similar for the different prey items. Although handling times vary dramatically among prey types in some shorebird foraging systems (e.g. Zwarts et al. 1996), in this case all prey items are taken whole without the need for shell removal, so handling time is likely to be relatively uniform. The results of the present study were qualitatively unaffected even when extreme selection of the most energy rich prey types was assumed. It is unlikely, however, that foragers could achieve very high levels of selection in most cases, because the most energy rich prey type in intertidal habitats (littorinids) was relatively rare (see table 2.1).

Given that the energy expenditure of free-living ruddy turnstones approaches the metabolic ceiling (Piersma & Morrison 1994, Morrison et al. 1997, Piersma et al. 2003), we would predict strong selection of the most profitable foraging substrates. The fact that ruddy turnstones appear to spend only a limited amount of time foraging on highly profitable supratidal habitats implies that there is some cost associated with supratidal feeding. Costs could include increased parasitic infection (Norris 1999, Le Drean-Quenec'hdu et al. 2001), elevated predation risk (Whitfield 1985b, Hilton et al. 1999a), disturbance, and nutritional limitation (Boutin 1990, Martin 1987). Further

work is required to resolve these possibilities and understand why the distribution of foraging ruddy turnstones among alternative foraging substrates does not reflect the quality of those habitats.

Chapter 3: The structure and dynamics of beach-cast wrack

3.1 Introduction

It is becoming clear that many shorebirds commonly regarded as intertidal specialists forage in both intertidal and supratidal habitats. Consensus is emerging that foraging shorebirds use supratidal habitats, often over the high water period, when energy intake during the low water period has been inadequate (Goss-Custard et al. 1996, Caldow et al. 1999, Dann 1999, Masero et al. 2000, Stillman et al. 2000b, Smart & Gill 2003), and furthermore, changes in supratidal foraging have been linked to energetic requirements (Goss-Custard 1969, Zwarts et al. 1990, Velasquez & Hockey 1992) and intertidal habitat change (Tsai 2001). However, the natural dynamics of supratidal foraging resources have received very little attention in the literature, despite the fact that understanding the relationship between these resources and decisions made by foragers could throw much light on the adaptive significance of such habitat switching. Accurate interpretation of supratidal foraging patterns is very difficult without information on variation in supratidal resource characteristics. This chapter describes the natural dynamics of potentially one of the most important supratidal foraging resources for shorebirds, namely beach-cast wrack.

Deposits of beach-cast wrack, here defined as discrete aggregations of marine vegetation, algae or the like, cast ashore by wave action, occur commonly along sea coasts, and are important components of productivity and nutrient cycling in littoral systems (Koop et al. 1982, Hansen 1984, Bergerard 1989, Kirkman & Kendrick 1997, Rossi & Underwood 2002). Beach-cast wrack is particularly important in supplying nutrients to a part of the shoreline with little resident primary production (McLachlan et al. 1981, Colombini et al. 2000). For example, up to 19% of seagrass production in a Kenyan lagoon passed through a beach-cast phase, contributing to local cycling of the nutrients tied up in their tissues (Ochieng & Erftemeijer 1999). Much of this nutrient supply is lost rapidly from beaches through wave action,

but some is retained interstitially in the sediment or enters the macrofaunal food chain (Brown & McLachlan 1990). These effects will be particularly strong in beach-cast wrack, where material cast onto the beach undergoes bacterial decomposition over a period of up to several weeks. Beach-cast wrack could therefore provide an important supratidal food resource for shorebirds in close proximity to their intertidal foraging and supratidal roosting habitats.

During the various stages of its decomposition, beach-cast wrack supports a rich and dynamic, but relatively understudied fauna (Behbehani & Croker 1982, Berzins 1984). Wrack flies (Diptera: Coelopidae) are dependent on beach-cast wrack for completion of their life cycle (Blanche 1992), and usually vastly outnumber other inhabitants of beach-cast wrack in temperate Europe (Backlund 1945, Egglishaw 1965). Most studies of beach-cast wrack fauna have therefore concentrated on coelopids (Egglishaw 1960, Phillips et al. 1995a,b Hodge & Arthur 1997, MacDonald & Brookfield 2002), although some have considered amphipods (Behbehani & Croker 1982, Marsden 1991), Coleoptera (Keys 1918), mites (Halbert 1920) and assemblages more generally (Backlund 1945, Egglishaw 1965, Hansen 1984, Bergerard 1989, Inglis 1989, Colombini et al. 2000). The scattered literature on beach-cast wrack faunal studies awaits thorough review, but the general picture is that the size and composition of faunal assemblages vary dramatically with the algal species involved, geographical location, local topography, climate, tidal cycle and season, such that few generalisations can be made about the quality and predictability of these habitat patches for foraging shorebirds.

The literature on the use of beach-cast wrack by shorebirds is extremely scant, despite suggestions that it may be an important foraging substrate and a plea for further research by Kirkman & Kendrick (1997). There are brief anecdotal reports of several bird species feeding on invertebrate colonisations within rotting beach-cast wrack (e.g. Backlund 1945, Egglishaw 1965, Jones 1975, King 1978, Dobson 1997), but very few quantitative studies on the dynamics of this habitat, and its importance for wintering shorebirds. In a study on the Californian coastline, numbers of black

turnstone *Arenaria melanocephala* (Vigors) and ruddy turnstone, the only shorebird species present in the study area that used beach-cast wrack, increased after populations of a subtidal macroalga were restored, while numbers of other species did not change (Bradley & Bradley 1993). The authors suggested a positive relationship between the amount of beach-cast wrack and shorebird density, although the conclusion must be regarded as tentative as no direct measurements of the availability or quality of beach-cast material were made before or after the change in macroalgal populations.

Patch choice decisions by foragers depend crucially on the profitability (Charnov 1976, Milinski 1979a) and predictability of alternative possible patches (Caraco et al. 1980, Stephens 1981, Stephens & Charnov 1982), not least because more profitable patches may incur costs associated with density-dependence (Fretwell & Lucas 1970, Shorrocks et al. 1979, Sutherland et al. 1988) and predation risk (Caraco 1979, Gilliam & Fraser 1987, Brown 1988). To understand the decisions of foragers using any resource, the first step therefore, must be to quantify spatial and temporal variation in the quantity and quality of the resource. It has been suggested that shorebirds feed over high water on invertebrates within deposits of beach-cast wrack as a supplementary food source to "top-up" inadequate low water food intake (Eaton 2001). However, there are several other explanations for this behaviour (see chapter 6). The "topping-up" hypothesis rests implicitly on a number of as yet untested assumptions about how birds respond to variation in the extent and profitability of these supratidal food resources.

Beach-cast wrack is generally variable in its extent over time (Bergerard 1989, Kirkman & Kendrick 1997, Ochieng & Erftemeijer 1999), but spatial and temporal variation in its profitability for foraging shorebirds is currently unknown. This chapter describes the extent of beach-cast wrack deposits as a foraging habitat for shorebirds, their ontogeny, and the characteristics of invertebrate colonisations. Spatial and temporal patterns of habitat availability and quality are also described.

3.2 Methods

3.2.1 Beach-cast wrack

This work was conducted on an east-facing, 39.5 km stretch of coastline between St. Mary's Island (55º 4' 37"N 1º 27' 8"W) and Amble (55º 19' 60"N 1º 34' 60"W), on the north-east coast of England during winter 2000/2001 (see figure 1.1 on page 4). Winter throughout is defined as the months of November to February inclusive, a period when migratory activity of shorebirds in the study site is minimal and populations are stable (Eaton 2001). Data collection was restricted to this period to reflect most accurately the habitat choices faced by wintering shorebirds in the study site, and because variation in daylength was limited.

The appearance of all beach-cast wrack within the study site was monitored during weekly visits made for 16 weeks throughout the winter study period. Each deposit was uniquely identified so it could be tracked over time. A wrack deposit was defined as an aggregation of algal and other beach-cast material above the most recent high tide mark sufficient to form a coherent mass of at least 10 m in length and 1 m in width (equivalent to the "wrack banks" of Backlund 1945). This meant that incoherent strandline debris not forming a distinct mass of at least these dimensions was excluded (the "wrack strings" and "wrack flakes" of Backlund 1945). This definition seemed to make biological sense, as large numbers of colonising invertebrates were observed only in such coherent wrack deposits. Deposits were considered distinct if they were separated by a gap of more than 10 m, or a physical barrier (such as a groyne or sluice). If a deposit was suspended and then re-deposited between weeks, it was also treated as a new unit as the process of invertebrate colonisation would have to restart (Egglishaw 1965). For each deposit, the following was measured: width to the nearest metre and height to the nearest 5 cm at 10 m intervals along the deposit; temperature (taken at 10 cm depth in the centre of the deposit at 10 m intervals); shape (tapered or symmetrical in cross section); and the presence or absence of strandline

debris in the vicinity of the deposit. The composition of the deposit was recorded by estimating percentage volume of the macroalgae *Fucus* and *Laminaria*, other algae, leaves from terrestrial plants, sand, coal, stones and bryozoan mats.

The study site was divided into 79 sections each of 500 m, and the section in which each deposit formed was recorded. Based on 1:10000 maps (Ordnance Survey data, 1991), the aspect of each section was recorded as north-east, south-east, south-west, or north-west, and the distance from each section to the nearest area of rocky intertidal was measured. The frequency of beach-cast wrack appearance in each section was calculated by summing the number of weeks in which beach-cast wrack was recorded in the section.

3.2.2 Weather data

Measurements of wind speed and wind direction were extracted from UK Land Surface Station weather data for Boulmer (10 km north of the study site at 55º 25' 0N 1º 35' 0W) obtained from the Meteorological Office via the British Atmospheric Data Centre (BADC, Space Science and Technology Department, R25 - Room 2.119, Rutherford Appleton Laboratory, Didcot, Oxfordshire, OX11 0QX, UK). Mean, maximum, minimum and standard deviations were calculated for the two weather variables by pooling data for the seven days prior to each measurement of beach-cast wrack. As the wind direction data were circularly distributed, calculation of these statistics for wind direction followed Zar (1999).

3.2.3 Invertebrate sampling

Samples of invertebrates were taken from two wrack deposits at Cresswell (55º 13' 44"N 1º 31' 41"W) on 27th November 2001 and one at St Mary's Island (55º 4' 14"N 1º 27' 10"W) on 11th January 2002. After measuring deposit width, depth, and temperature at 10 cm depth at the centre and seaward edge (temperature was only measured for the St Mary's Island deposit), litre samples of wrack were obtained in the centre, and at the

seaward edge every 10 m along each of the three deposits. This was done by placing a 10 cm*10 cm quadrat on the surface of the deposit, and cutting a 10 cm cube out of the material, using the quadrat as a guide. Based on over 400 observations of ruddy turnstones foraging on beach-cast wrack (see chapter 4), the maximum depth reached by the birds was estimated to be 10 cm, usually by excavating the substrate. Samples were removed from the wrack deposit and transferred to sealed containers as quickly as possible to minimise escape by invertebrates. They were then washed thoroughly over a 1 mm sieve and all invertebrates were removed. The numbers of each identified taxon (classified as either coelopid fly species or oligochaetes) in each sample were recorded, together with their life stage (larva, pupa, adult) in the case of coelopid flies.

3.2.4 Data analysis

Most statistical analyses were implemented in SPSS version 11 (233 S. Wacker Drive, 11th floor, Chicago, Illinois 60606). Data were transformed where appropriate. Because the relationship between deposit age and mean temperature was possibly dependent on deposit identity, it was investigated using simple linear regression with groups in Genstat version 5 (Genstat 5 Committee of the Statistics Department, Rothamsted Experimental Station, Harpenden, Hertfordshire, UK). A cumulative ANOVA was then used to determine whether there was evidence of non-parallelism among the regression lines.

3.3 Results

3.3.1 Extent of beach-cast wrack availability

Fifty deposits of beach-cast wrack were identified during the winter period, although 112 measurements of deposits were made in total, as some were present during more than one weekly survey. A mean of 7.0 deposits was

present each week (range: 2 - 13, SD = 3.3), and each week a mean length of only 1% of the coastline in the study area was populated with beach-cast wrack (mean weekly combined length of all deposits = 406 m, n = 16, range: 90 - 810 m, SD = 233.8 m; total coastline length 39500 m). The mean total area occupied by beach-cast wrack each week was 1821 m^2 (n = 16, range: 420 - 3500 m^2, SD = 1075 m^2, compare with 158,000 m^2, the area of a strip along the coastline 4 m wide, the average width of the wrack deposits). Beach-cast wrack therefore formed an extremely small proportion of possible supratidal foraging habitat.

3.3.2 Characteristics of individual deposits

Deposits of beach-cast wrack were generally clearly distinguishable from surrounding habitat except when material was in the process of deposition. Boundaries of deposits were typically abrupt, although in 78% of cases, scattered algal debris was present in the vicinity of the main deposit. Summary statistics for the 50 deposits are given in table 3.1. See Appendix 2 for data on individual deposits. The high coefficients of variation indicate large variation in deposit characteristics.

Table 3.1 Physical characteristics of the 50 beach-cast wrack deposits recorded during winter 2000/2001 in the study area. Where a particular deposit was measured more than once because it was present during more than one weekly sampling period, values were averaged.

	Mean	Range	SD	CV
Length	54.3 m	10-125 m	29.5	0.54
Volume	55.0 m^3	1.3-433.5 m^3	70.34	1.28
Area	236.7 m^2	17.3-1011.5 m^2	198.66	0.84
Depth	0.35 m	0.13-0.98 m	0.20	0.57
Temperature	8.42 ºC	4.15-16.23 ºC	3.09	0.37

The major constituents of beach-cast wrack were *Fucus* spp (mainly *F. serratus*, but also *F. vesiculosus* and *F. spiralis* L.), forming on average 60%

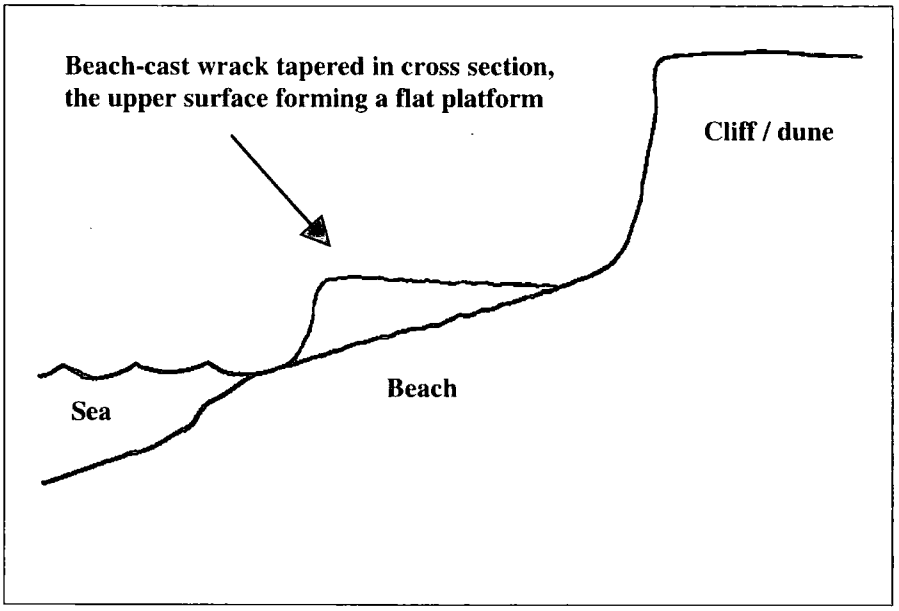
of each deposit, and *Laminaria* spp (mainly *L. digitata* (Hudson), but also *L. hyperborea* (Gunnerus) and *L. saccharina* (L.) Lamouroux), comprising about 25%. Average composition of the deposits is given in table 3.2.

Table 3.2 Composition of beach-cast wrack deposits. Figures are mean percentage compositions by volume. Where a particular deposit was measured more than once because it was present during more than one weekly sampling period, values were averaged.

Constituent	Mean	Range	SD
***Fucus* spp**	60.0	10-95	19.5
***Laminaria* spp**	24.7	0-70	14.4
Leaves of terrestrial plants	8.3	0-85	21.4
Sand	2.6	0-50	9.4
Coal	2.6	0-50	8.9
Stones	1.5	0-40	5.4
Bryozoans	0.3	0-30	2.9
Rhodophytes / Chlorophytes	0.1	0-10	1.0

Eighty-eight percent of beach-cast wrack deposits were tapered in cross section, with the tallest part nearest the water's edge (figure 3.1 shows a typical deposit diagrammatically). Potential foraging substrate for shorebirds would therefore consist of a level platform, with the depth of substrate increasing toward the shoreline. Deposits typically occurred above the high water mark, and the mean height of deposits above ordnance datum each week was greater than the height of high tide (Wilcoxon signed ranks test: $Z = 1.99$, $n = 16$, $p = 0.047$). There was frequently a vertical drop-off at the seaward edge of the deposit (figure 3.1).

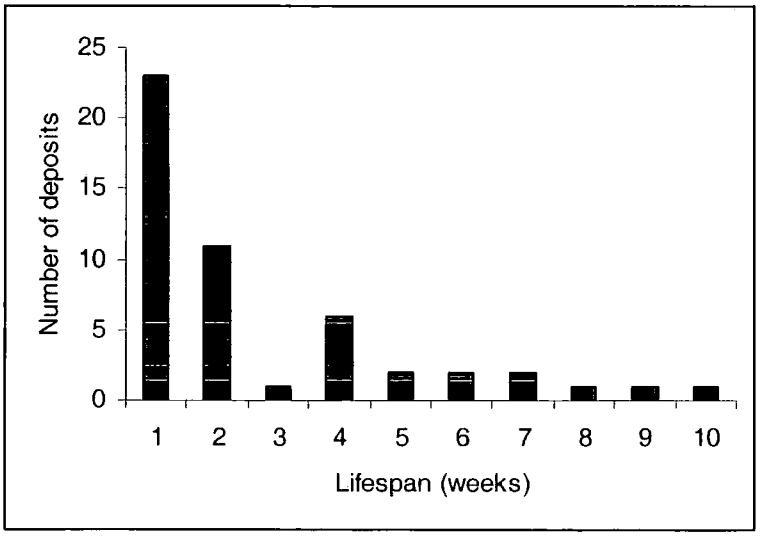
Figure 3.1 A typical beach-cast wrack deposit.



3.3.3 Beach-cast wrack ontogeny

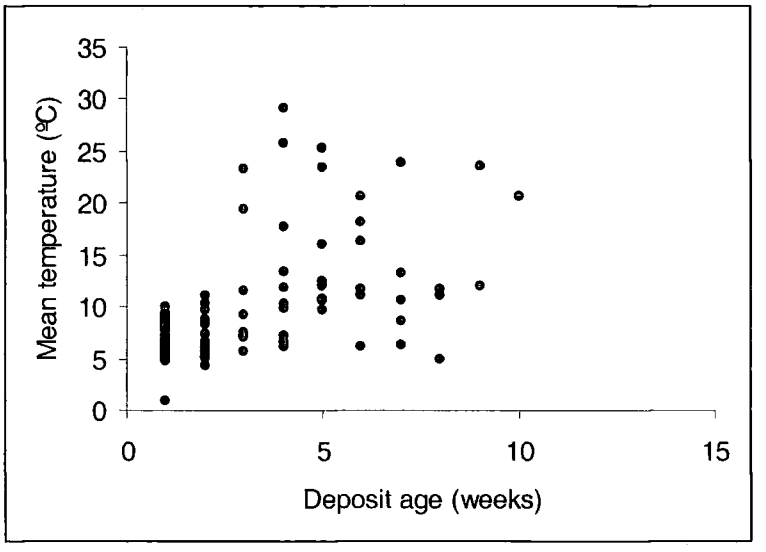
The mean lifespan of beach-cast wrack deposits was 2.7 weeks (18.9 days), although the distribution was highly right skewed, with 46% of deposits observed on only one occasion (figure 3.2). Lifespan of beach-cast wrack deposits was uncorrelated with mean deposit width, length, volume and area (all $r_s < 0.6$, $n = 112$, all $p > 0.05$).

Figure 3.2 Frequency distribution of deposit lifespans. Mean lifespan was 2.7 weeks (n = 50, SD = 2.36; range: 1-10).



Mean temperature of a deposit increased with age (figure 3.3, simple linear regression with groups; $F_{1,33} = 37.08$, $p < 0.001$). There was no evidence for non-parallelism among the regression slopes introduced by considering deposit identity ($F_{41,33} = 0.79$, $p = 0.767$), and the individual regressions did not require separate intercepts ($F_{22,33} = 1.2$, $p = 0.314$). No deposit achieved a mean temperature of above 15 ºC until it had been recorded on at least three consecutive weekly surveys, i.e. until it was aged between two and four weeks.

Figure 3.3 The relationship between deposit age and temperature (n = 98). Age is expressed in cumulative number of weekly surveys in which a deposit had been recorded, and temperature is the mean value of measurements taken at a depth of 10 cm in the centre of the deposit every 10 m along its length. See text for statistical analysis.



3.3.4 Predicting invertebrate density

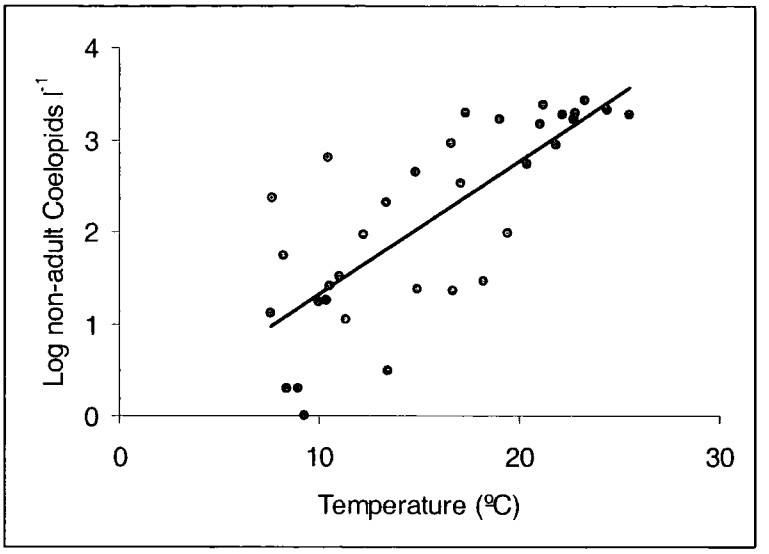
Samples from beach-cast wrack contained adult, larval and pupal stages of coelopid flies, together with smaller numbers of oligochaetes. The distribution of the invertebrates appeared uniform throughout each sample, although varied widely between samples. Mean density of coelopid larvae was 413 l^{-1} (range 0 - 2600, SD = 664.5), pupae 29.3 l^{-1} (range 0 - 400, SD = 74.2), and adults 0.6 l^{-1} (range 0 - 6, SD = 1.4). The maximum number of non-adult

coelopids in a sample was 2609 in a sample with a temperature of 23.3 ºC. The mean density of oligochaetes was 144 l^{-1} (0-1300, SD 277.7). Oligochaete numbers were relatively low, and their average biomass was less than a tenth of that of coelopid larvae (estimated mean volume of oligochaetes: 814 $mm^3 l^{-1}$; coelopid larvae: 17516 $mm^3 l^{-1}$). Furthermore, shorebirds appeared to concentrate exclusively on coelopid flies, particularly larvae and pupae (see chapter 4). Consequently, subsequent data refer only to coelopids. The frequency distribution of coelopid numbers was strongly right skewed, many samples containing few or no fly larvae. This indicates a patchy distribution of coelopids across the deposits. Position on the deposits was important; mean density of coelopids of all life stages in samples taken from the centre of the deposit were more than four times greater than that of samples from the edge of the deposit (paired t-test, $t = 4.28$, d.f. = 32, $p < 0.001$). This was almost certainly driven by temperature, which dropped from a mean of 19.3 ºC in the centre to 12.0 ºC at the edge (paired t-test, $t = 4.43$, d.f. = 16, $p < 0.001$). The drop in temperature did not vary with deposit width ($r = 0.15$, $n = 17$, $p = 0.560$).

After investigating a maximal linear regression model including temperature, depth and width of the deposit at each sampling point, temperature was retained in the final model as the only significant predictor of the density of non-adult coelopids ($F_{1,32} = 45.61$, r2 = 0.58, $p < 0.001$, figure 3.4), although it explained little of the variation in the number of adult flies in the samples ($F_{1,32} = 0.35$, $p = 0.559$). Because the relationship between temperature and density of coelopid larva appeared non-linear (figure 3.4), a sigmoidal gompertz curve was fitted to the data and compared with the simple linear model. The linear model was chosen as it outperformed the non-linear model (non-linear model: $F_{3,30} = 15.08$, $r^2 = 0.56$). The linear regression equation for non-adult coelopids was:

$$1 + (\log_{10} \text{COELOPID}) = (0.147 * \text{TEMP}) - 0.185 \qquad \textbf{(Equation 1)}$$

Figure 3.4 The density (individuals per litre) of non-adult coelopids increased with temperature. See text for statistical analyses.



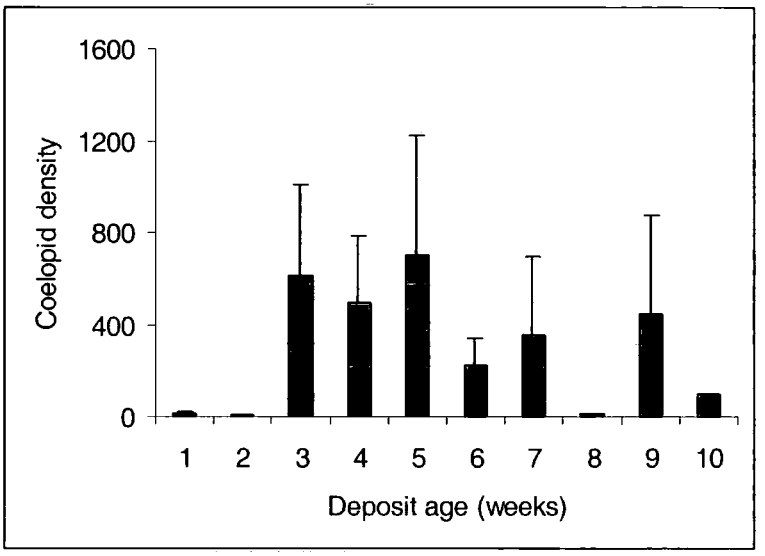
3.3.5 Predicting patch quality

The relationship between temperature and coelopid density derived from the sampling data was used to predict patch quality (i.e. non-adult coelopid density) using the temperature measurements taken from beach-cast wrack deposits throughout the winter period. The predicted density of non-adult coelopids was calculated by splitting each deposit into slices every 1 m along its length and assuming that the temperature, height and width of the deposit changed linearly along each 10 m section between the measured points. Temperature was also assumed to change linearly from the centre to the edge of the deposit using a proportional decline from the centre to each edge of 0.38 derived from the sampling data. The number of non-adult coelopids in the surface 10 cm of each 1 m slice was then calculated from equation (1). These values were then aggregated to provide summary coelopid density statistics for each deposit (see Appendix 2).

Overall predicted mean density of non-adult coelopid flies in beach-cast wrack deposits was 212 flies l^{-1} (range: 2 - 4302, SD = 716.0). Estimated mean coelopid density began to increase significantly only after a deposit had been present for 3-5 weekly surveys (see figure 3.5), but remained

relatively constant after this. The error bars indicate a great deal of variation in the predicted density of coelopids.

Figure 3.5 Changes in the estimated density of non-adult coelopid flies during the development of beach-cast wrack deposits. Fly density is mean number of individuals per litre for all deposits of a given age. Error bars are ± 1 SE. Deposit age is expressed by the number of consecutive weekly surveys in which a particular deposit was recorded.



3.3.6 Spatial and temporal patterns in beach-cast wrack appearance

Deposits of beach-cast wrack appeared in the study site throughout the winter period but, as discussed above, they varied dramatically in size, shape and duration, as well as in density of colonising invertebrates. Typically, deposits occurred over sandy substrates, and most usually in the southern edges of bays where floating and suspended material was trapped. These topographical features appeared to limit suitable sites for the formation of beach-cast wrack. Indeed, deposits occurred in only 18 of the 79 divisions of the study site, and the frequency distribution of the number of weeks in which beach-cast wrack was present in each section was strongly right skewed (skewness = 3.24, SE = 0.27). One north-facing division just north of St Mary's Island continuously held beach-cast wrack for all 16 weeks throughout the winter period. Observed and expected frequencies of beach-cast wrack

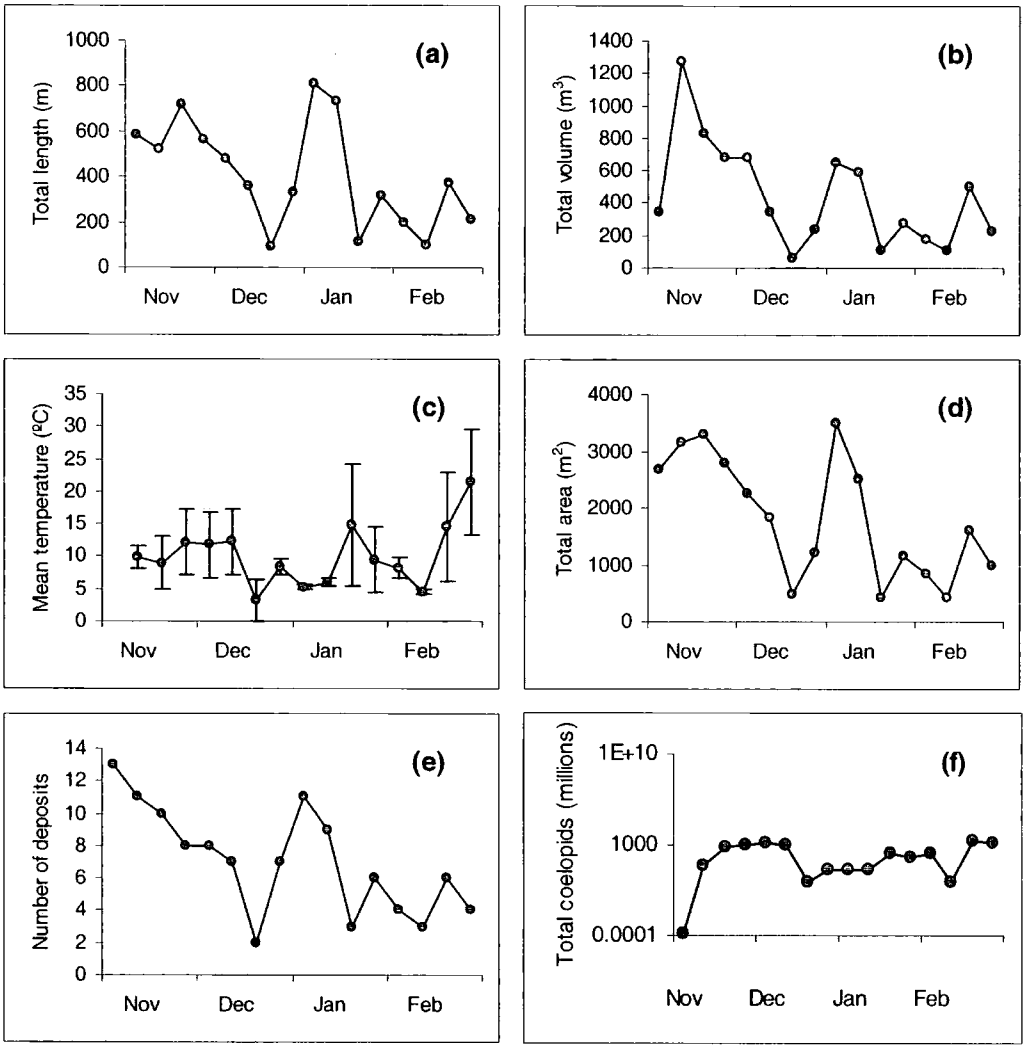
appearance did not change with aspect (G-test using frequency of beach-cast wrack appearance in the four compass directions: $G_{adj} = 2.86$, $p = 0.240$). The frequency of beach-cast wrack appearance was greater on sandy divisions of the study site than rocky divisions ($G_{adj} = 7.9$, $p = 0.005$), and declined with distance from the nearest area of rocky intertidal ($r_s = -0.47$, $n = 79$, $p < 0.001$), with no beach-cast wrack appearing at all in the 30 divisions of the study site more than 500 m from an area of rocky intertidal.

Spatial homogeneity of the frequency of beach-cast wrack appearance was tested using simple autocorrelation analysis, thus treating the data as evenly spaced points along a line. There were no significant autocorrelations or partial autocorrelations at any lags ($n = 79$, all $p > 0.05$). Furthermore, characteristics of individual deposits showed no obvious temporal pattern over the winter period (figure 3.6), and there was no significant temporal predictability based on autocorrelation and partial autocorrelation analyses of the weekly data ($n = 16$). Variables investigated were total number of deposits, total length, total volume, mean area, mean depth, and mean deposit temperature.

3.3.7 Predicting beach-cast wrack from weather conditions

None of the wind speed or wind direction measures was correlated with the extent (length, volume, surface area) or quality (temperature, predicted coelopid density) of beach-cast wrack (wind speed data all $p > 0.2$; wind direction data all $p > 0.05$).

Figure 3.6. Variation in beach-cast wrack characteristics over the winter period. (a) Total length of all deposits combined; (b) total volume of all deposits combined; (c) mean temperature ± 1 SD; (d) total surface area of all deposits combined; (e) number of deposits; (f) total predicted number of non-adult coelopid flies available in the study site.



3.4 Discussion

Beach-cast wrack comprised a small proportion of overall possible supratidal foraging substrate in terms of surface area, but the high densities of colonising invertebrates suggest it could form an important resource for foraging shorebirds.

There was great variation in deposit size and quality over time, but variation across space was much more limited, with only 23% of the 500 m sections of the study site hosting beach-cast wrack at least once during the winter period. This was not simply due to beach-cast wrack being a rare phenomenon, as deposits were recorded on 112 occasions during the study. If foragers could respond to environmental cues that predict a high likelihood of beach-cast wrack on a given stretch of coast, or learn the locations of these areas over time, much of the spatial uncertainty could be removed. For example, the sections in which beach-cast wrack occurred were overwhelmingly those containing or close to rocky intertidal areas. Possible explanations for this are that most material comprising the deposits was derived locally, deposition of drifting algae was favoured close to areas of rocky intertidal, or a combination of these.

Areas near rocky intertidal outcrops may favour deposition of suspended algae, perhaps for topographical or hydrographical reasons. In a study conducted in Western Australia, floating drift cards (simulating transport of buoyant algae such as *Fucus* spp) travelled a mean distance of 9.3 km (1.8 - 40.8 km) from the release site, and negatively buoyant drift cards (simulating transport of kelps e.g. *Laminaria*) a mean distance of 4.6 km (0.8 - 29.6 km; Kirkman & Kendrick 1997). The Northumberland coast is an area of high natural dispersion (Hiscock 1998), suggesting that detached algae will drift similar or greater distances than in the Australian study. It therefore seems unlikely that all beach-cast wrack in the present study originates from within 500 m of the deposition site. Outcrops of hard rock erode more slowly than the intervening soft-sediment coast, forming headlands that extend into the sea, and there is a southerly current stream along the Northumberland coast (Evans 1957, 1959), suggesting that material is likely to be deposited in the north-facing lips at the southern end of bays. This may explain why the north-facing bay at St Mary's Island held beach-cast wrack continuously for the winter period. Indeed, this site has been used several times for the study of beach-cast wrack fauna (Egglishaw 1958, Phillips et al. 1995a), presumably because of this propensity to receive beach-cast material and retain it for extended periods. In terms of supratidal foraging by rocky-shore specialist

shorebirds, it is possible therefore that proximity to areas of rocky intertidal could be used as a cue for birds searching for supratidal foraging opportunities.

Despite the *spatial* tendency for beach-cast wrack to form near areas of rocky intertidal, the pattern of its availability over *time* was highly unpredictable. In particular, the availability of material in one week could not be predicted from availability in previous weeks or from weather conditions. This means that although topographic features associated with high beach-cast wrack availability could in principle be identified or learnt by foraging shorebirds, there were no obvious predictors of temporal variation in beach-cast wrack availability.

The most likely fate for a given patch of newly deposited algae was resuspension without any significant invertebrate colonisation. Colonisations occurred only in deposits that remained undisturbed for two or more weeks, but from the point of view of a foraging bird, any given deposit could not relied upon to remain intact from one tidal sequence to the next. The mean lifespan of beach-cast wrack deposits in this study was 19 days, and complete decomposition of an undisturbed deposit of the kelp *Ecklonia radiata* in Western Australia took 20 - 23 days (Kirkman & Kendrick 1997). The present study shows that in general, beach-cast wrack is highly ephemeral and may frequently be resuspended before colonisation by invertebrates. The life cycles and population genetic structures of beach-cast wrack fauna reflect the frequent occurrence of catastrophes and the need for extreme opportunism (Egglishaw 1965, Leggett et al. 1996). The foraging strategies of predators must to a certain extent show equivalent flexibility.

Once decomposition of beach-cast wrack was underway, some very large colonisations by coelopid wrack flies were observed. Densities of over 2600 non-adult flies per litre were observed in samples of beach-cast wrack, and even greater densities are reported in the literature (Egglishaw 1960). Beach-cast wrack is therefore potentially a highly profitable foraging substrate for shorebirds. Furthermore, the quality of patches of beach-cast wrack for

foraging shorebirds can be estimated fairly accurately by using the relationship between temperature and density of coelopid flies. The regression model used here assumed for parsimony that this relationship was linear, although this may not be the case in reality, particularly at extremes of temperature. Two species of coelopid fly, *Coelopa pilipes* Haliday and *C. frigida* (Fabricius), occur commonly in north-east England. The latter is adapted for cooler temperatures, and the relative density of the two species between 20 ºC and 33 ºC is determined by temperature-mediated competition; below 20 ºC only *C. frigida* survives, and above 33 ºC, only *C. pilipes* survives (Phillips et al. 1995b). In addition, there are likely to be temperature thresholds below which larval development is severely retarded and above which competition inhibits further population growth. Additionally, the model may over-predict coelopid densities in cool deposits because it was based on deposits with a wide range of temperatures, in which larvae could migrate from warm areas to cooler areas in which development would not normally commence. Despite these caveats, however, the most parsimonious way to describe these data statistically was with a linear model, and this model fitted the relationship very well. Predicted invertebrate densities are therefore likely to reflect at least broadly the dynamics of patch quality for foraging birds.

There was no relationship between temperature and the number of adult flies in samples of beach-cast wrack. Adult wrack flies are the dispersive stage in the life cycle, often emerging in large numbers and performing mass emigrations from habitat patches (Egglishaw 1961). Adult flies reach new deposits and begin the colonisation process once again. Adults are known to use temperature as a cue when choosing egg-laying sites (Phillips et al. 1995b), but presumably they explore the deposit looking for regions of appropriate temperature before laying. Also, some adult flies may have escaped during the process of collecting samples from beach-cast wrack. These factors may lead to substantial scatter in the relationship between temperature and the density of adult coelopids.

This study has shown that at appropriate stages of maturity, beach-cast wrack is potentially a very rich food source for those foraging shorebirds able to exploit it, and that beach-cast wrack containing large invertebrate colonisations is available for a significant proportion of the winter period. However, the extent and quality of the resource are apparently unpredictable over time. For foraging shorebirds, beach-cast wrack deposits appear to form an unpredictable element (both in terms of habitat quality and availability) within a matrix of otherwise predictable intertidal foraging.

The results of this chapter raise questions about how the presence of a profitable but unpredictable substrate influences patch-choice decisions by foragers. For example, the availability of beach-cast wrack might directly affect foraging effort (e.g. the relative proportion of time spent searching for food and engaged in vigilance) put in by birds during the intertidal phase.

Chapter 4: Patterns in vigilance, group size and foraging behaviour among substrates that vary in profitability, predictability, and predation risk

4.1 Introduction

4.1.1 The group size effect

Foragers often reduce individual predation risk by forming larger groups (Hamilton 1971, Pulliam 1973, Milinski & Heller 1978; see Krause & Ruxton 2002 for a review), particularly when foraging in risky situations (Hager & Helfman 1991, Tegeder & Krause 1995, Spieler 2003). Such responses to predation risk can occur at a variety of temporal scales, from seasonal changes (Werner 1986, Lucas et al. 1996), down to daily changes and beyond (Dodson 1990, Dill & Gillett 1991). Forming larger groups under elevated predation risk benefits the forager because the vigilance effort required of individuals usually declines as group size increases (Lima 1995). There are two main hypotheses to explain this group size effect. Firstly, when there are more individuals in a foraging group, a smaller individual contribution is required to maintain a given level of overall group vigilance (Pulliam 1973, Powell 1974, Bertram 1980, Elgar 1989). This effect is usually measured by the interscan interval, the time period between successive initiations of vigilance postures within the group (Pulliam 1973, Bednekoff & Lima 1998, 2002). Secondly, the reduction in individual predation risk through numerical effects such as dilution (Foster & Treherne 1981), predator confusion (Milinski 1979b) and cooperative warning and escape effort (Humphries & Driver 1967, Proctor et al. 2003) imply that a lower level of overall group vigilance is required when foraging in larger groups, all else being equal.

Although this reduction in overall group vigilance with increasing group size has been well documented (Barnard & Thompson 1985, Elgar 1989, Lima 1990, Lima & Dill 1990, Quenette 1990, Cresswell 1994, Roberts 1995), a

growing number of recent studies has reported no detectable effect of group size on individual vigilance levels (Catterall et al. 1992, Scheel 1993, Jones 1998, Krams 1998, Treves 2000). Furthermore, Roberts (1996) has pointed out that many variables might confound the relationship between group size and individual vigilance. For example, interpreting a meta-analysis of group size and vigilance in primates, Treves (2000) found scant evidence for the group size effect in mammals and, among other suggestions, proposed that vigilance will not decline with group size in situations where predators do not rely on surprise, because there is no benefit of collective decision-making and potentially a cost in terms of group conspicuousness. However, variation in predation risk itself could obscure or even reverse the relationship between group size and individual vigilance levels, even in situations where predators hunt by surprise.

Here, I consider a situation where the main risk of predation for foragers is from raptors hunting by surprise (Cresswell 1996). Foragers tend to form larger groups on high risk foraging substrates than on low risk substrates. Because group size and the probability that the group is attacked covary, the group size effect may be confounded in this situation. At the very least, this kind of system allows us to explore reasons for deviation from the group size effect, particularly where the high risk substrate is also profitable in terms of energy intake rate (see chapter 2). For any given group size, we might predict interscan interval to decrease under conditions of elevated predation risk; this requires individuals to modulate their own vigilance contribution based on the expected probability of a predator attacking the group. This would involve integrating clues from outside the group, as well as adjusting individual vigilance contribution to current group size. Although these effects can be distinguished experimentally, under natural conditions, elevated predation risk is frequently associated with higher profit foraging patches (Houston et al. 1993). Under these conditions, we might predict significant departures from the expected group size effect.

This chapter considers how the group size effect is influenced by variation in predation risk by comparing the relationship between flock size and vigilance

levels of ruddy turnstones foraging among several habitats that vary in predation risk. Intertidal habitats are much further from cover from which raptors can launch surprise attacks than are supratidal habitats (see chapter 6). Within intertidal habitats, foraging ruddy turnstones might be more visible to predators on pale, barnacle-covered rock than on darker, more mottled *Fucus*-covered rock (Metcalfe 1984). Foraging high up the shore is known to incur elevated predation risk in shorebirds (Whitfield 1985b, Hilton et al. 1999a), probably because supratidal habitats are much closer to cover than intertidal habitats, and coastal features such as cliffs further restrict the distance from which a predator's approach can be detected. Within supratidal habitats, predation risk is influenced more by distance to cover (Hilton et al. 1999a) than the conspicuousness of foragers to predators, so beach-cast wrack, which occurs closer to land than strandline debris (see chapter 1), should be a more risky foraging substrate in terms of predation risk.

If foragers are adjusting their vigilance levels to external predation risk over and above that predicted by flock size, interscan interval should vary predictably for a given group size effect depending on the predation risk associated with the different substrates. On supratidal habitats, we would therefore predict (a) larger flock sizes than on intertidal habitats and (b) a shorter interscan interval than predicted by the general group size effect alone. We would also predict excessive vigilance on the more dangerous versus the safer substrate (beach-cast wrack versus strandline and barnacle- versus *Fucus*-covered rocks) within the two broad habitat types. This could lead to departures from the expected reduction in vigilance with increasing group size, thereby demonstrating a confounder of the group size effect.

4.1.2 Diurnal patterns in vigilance

One reason foragers attempt to minimise their individual vigilance contribution is that scanning for predators conflicts with other important activities, such as searching for food, body maintenance and breeding behaviours (Dimond & Lazarus 1974, Caraco 1979, Lendrem 1983, Elgar 1989, Mooring & Hart 1995, but see Lima & Bednekoff 1999a, Guillemain et

al. 2001). The physiological state of foragers therefore has a major effect on the trade off between vigilance and foraging effort. Foragers in a poor physiological state should devote less time to vigilance than predicted by predation risk or flock size because starvation is a more immediate risk than predation. This effect has been modelled extensively, and has given rise to predictions about the pattern of mass gain during the course of a foraging bout (McNamara & Houston 1986, 1990, Houston et al. 1993, McNamara et al. 1994).

Providing that energy is assimilated at a greater rate than it is expended in acquiring and digesting food, the physiological condition of a forager will improve during the course of a foraging bout. In general, there will be an increase in vigilance as animals near satiation, because mortality through predation becomes progressively more likely than starvation (Milinski & Heller 1978, Krebs 1980, McNamara & Houston 1986, Ydenberg & Houston 1986). However, the timing and trajectory of mass acquisition, and hence vigilance levels, will depend on characteristics of foraging substrates, such as their profitability, relative predation risk, and the ability of the forager to take cover in risk-free locations (Houston et al. 1993, McNamara et al. 1994, Cresswell 1998).

Here, I compare the diurnal trajectories of energy intake and vigilance by ruddy turnstones between two habitats that vary in predation risk and predictability. Despite some circumstantial evidence of nocturnal foraging by ruddy turnstones (e.g. Clark et al. 1990, Robert et al. 1989, Schneider 1985), recent radiotracking data indicate that they rarely forage at night in the present study area (Eaton 2001). Supratidal foraging substrates are high quality, but temporally unpredictable resources (see chapter 3). Given that any particular supratidal foraging patch could be degraded or destroyed within a few hours by wave action, we might expect birds to acquire mass at a consistently high rate whenever the opportunity arises to forage supratidally. Moreover, because predation risk is relatively high on supratidal substrates, vigilance levels should increase through the day as foragers acquire mass, either because of increasing mass-dependent predation risk

(Witter et al. 1994, Metcalfe & Ure 1995, Bednekoff 1996), or because of the forager nearing satiation (Pravosudov & Grubb 1997,1998).

Rocky intertidal substrates, on the other hand, are low quality, but relatively stable temporally. Chapter 2 showed that potential prey items in intertidal habitats in the present study area have a lower energy content than prey items in supratidal habitats. Rocky-shore invertebrate populations are generally open, with rapid recovery from perturbation possible via recruitment from unaffected areas (Thompson et al. 2002), and invertebrate motility is necessarily two dimensional, with the rocky substrate preventing burrowing. Given that intertidal foraging conditions are relatively predictable, we might expect birds to delay mass acquisition until late in the day to minimise mass-dependent predation risk (Houston et al. 1988, 1993, Houston & McNamara 1993). This predicts a rise through the day in energy intake rate when foraging on intertidal substrates, peaking just before dusk. The predictions for vigilance are less clear. Late in the day, a forager is at much greater risk of mass-dependent predation, so should be more vigilant. However, because feeding rate is high later in the day, vigilance will necessarily be traded off with food acquisition behaviours. The most likely outcomes are that vigilance will remain stable or decline through the day on intertidal habitats.

It must be borne in mind that tidal state is not independent of time of day. In the present study area, spring low tides currently occur in the mornings, and spring high tides in the afternoons, although this pattern is not permanent, and will reverse in about 18 years. The above predictions about diurnal patterns in foraging and vigilance behaviours assume that suitable habitat is available. Analyses investigating diurnal patterns therefore controlled for tide height at the time of each observation to minimise these effects (see section 4.2.5).

The aims of this chapter are threefold. Firstly, it presents comparative information on ruddy turnstones foraging on alternative substrates that differ with respect to predictability, profitability and predation risk. Secondly, it investigates the effects of variation in patch quality and predation risk on the

relationship between individual vigilance and group size, and then asks whether these effects translate into flock-level disparities. Consideration of wholesale variation in predation risk among alternative foraging patches should explain deviations from purely group size effects. Thirdly, it describes the diurnal patterns of energy intake and vigilance levels in birds foraging on the alternative substrates. These data are used to test predictions arising from state-dependent models of the trade-off between starvation and predation.

4.2 Methods

Data were collected between 5 November 2001 and 4 February 2002 at a wide range of sites, times of day, tidal states and weather conditions along the coastline of Northumberland, NE England (see chapter 1 for details of the study area). Disturbance to birds was significant at weekends (RF, unpub. data), so data were collected on weekdays to minimise any effects of disturbance on ruddy turnstone foraging patterns.

4.2.1 Flock measures

Flocks of foraging ruddy turnstones were observed in intertidal and supratidal habitats. Foraging birds were approached carefully and watched at a range of 50 - 100 m through a tripod-mounted Optolyth telescope using 20 - 60x magnification. If observer-related disturbance to the flock was apparent, such as birds leaving the flock or moving away from the observer, the observer retreated and selected a new flock. A flock was defined as a group of birds all connected by a maximum nearest neighbour distance of 10 m. To allow calculation of overall flock density, the number of ruddy turnstones comprising each flock and the approximate area occupied by the flock were noted. All distances were estimated to the nearest metre by reference to known distances between natural features.

The substrate on which the flock was foraging was recorded as *Fucus*-covered rock, barnacle-covered rock, strandline sand/debris, or beach-cast wrack. Although ruddy turnstones did use some other foraging substrates in the study area (see chapter 3), the use was too infrequent to allow adequate sample sizes to be obtained. If a flock switched substrate, or was followed from one tidal state to another, it was treated as a new observation. See chapter 1 for definitions of tidal states, and definitions of strand and beach-cast wrack foraging substrates. Flock membership and boundaries were to a certain extent dynamic, particularly in supratidal habitats, so average flock values were calculated from a series of at least five measurements to obtain stable estimates.

4.2.2 Individual foraging measures

Each flock was allowed five minutes to settle before foraging data were collected. A focal bird was selected at random from the flock. If it was colour-marked, the combination was recorded. Local forager density around the focal bird was calculated by estimating the number of other ruddy turnstones within an estimated 5 m radius of the focal bird. For flocks foraging on strandline debris and beach-cast wrack, the position of the focal bird within the flock was recorded as central or peripheral. A bird was considered to be central in the flock if it was completely surrounded by other birds, and peripheral if on the outermost edge of the flock, but within 1 m of a conspecific. Each focal bird was observed for 30 seconds while the following were noted (see below for definitions): number of pecks, number of meals obtained (allowing calculation of the number of pecks required per meal), number of head-ups, and number, polarity and outcome of aggressive encounters. If the bird went out of view for any part of the 30-second period, the observation was stopped, and a new focal bird selected.

A peck was defined as an attempt by the bird to capture a prey item. It was therefore distinct from a bill movement to bulldoze seaweed, turn stones, or clear away debris. For example, a bird feeding on *Fucus*-covered rocks would typically perform bill movements to flip seaweed to one side, and then

execute a series of pecks to capture exposed and disturbed prey items. All birds were observed through a telescope at up to 60x magnification, and it was usually possible to decide confidently whether a food item had been consumed following a peck. Frequently, the item was directly observable in the bill of the bird, or the bird's throat would bulge noticeably as the item was swallowed. Where it could not be ascertained with a high degree of confidence whether a food item had been ingested following a peck, the number of meals was not recorded for that particular bird, but the 30-second observation period was continued for the collection of the other behavioural data. It was generally not possible to identify prey items, as they were often small and visible only briefly. However, for birds foraging on beach-cast wrack, prey items were frequently identifiable as the larvae or pupae of coelopid wrack flies.

Head-ups were recorded to provide a measure of vigilance for predators or competitors as distinct from visual searching for foraging areas or food items. Postures in which the bird's head was raised accompanied by very limited interruption of the forager's walking rhythm, the head remaining in a vertical orientation, and limited scanning eye movements (where possible to discern this) were interpreted as food searching-related behaviour. Postures in which the bird's head was raised accompanied by an interruption of the search path of the bird, tilting of the head and / or scanning eye movements, were interpreted as vigilance for predators and / or competitors, and recorded for the purposes of this study as head-ups. The distinction between these two postures was usually easy to make in the field. If a bird made an ambiguous posture, such as a tilted head with scanning eye movements, but with an apparently uninterrupted search path, the observation period was stopped, and a new focal bird chosen.

A measure of overall flock vigilance was calculated. The average time elapsed between any member of the flock initiating a head-up posture was calculated as follows. First, mean flock size was multiplied by the mean number of head-ups performed by individuals comprising the flock. Thirty divided by this value gave the interscan interval i.e. the average gap in

seconds between the initiation of successive head-ups by any member of the flock. As head-up postures had non-zero duration, the interscan interval represented only the time period between initiation of vigilance postures (or the probability of any one individual initiating a vigilance posture) rather than the period when no bird in the flock was scanning for predators. A detailed investigation of head-up duration was beyond the scope of the current study, and to use an estimated mean value for head-up duration would simply subtract a fixed value from the current measure rather than add explanatory power. A further assumption of this method is that head-up postures are initiated by individuals at random with respect to other individuals within the flock. In the context of this analysis, this assumption is justified because the aim of calculating interscan interval here is simply to consider average vigilance in flocks as a whole, rather than patterns of vigilance contributions by individuals. Flocks with sample sizes less than five were excluded from the calculation of the interscan interval because mean head-ups could not be estimated with acceptable precision. Also, the one flock with a frequency of zero head-ups was excluded, as the probability of initiating a head-up posture could not be calculated. Sufficient data were available to calculate interscan interval for 44 flocks.

After each 30-second observation period, a new focal bird was chosen and the process repeated, the flock measurements being updated as necessary. Two observers collected observational data on pecks, head-ups, and aggressive interactions. One observer, the more experienced, also collected data on the number of meals consumed. Before data collection commenced, each observer independently scored the frequency of pecks, head-ups and aggressive interactions for the same 20 focal birds following the protocol above to allow repeatability to be checked. Because two observers took measurements, standard intraclass correlation was not an appropriate measure of repeatability (Lessells & Boag 1987). The degree of correspondence between the two observers' scores was therefore assessed using the slope, intercept and R^2 values from a linear regression analysis. Following Zar (1999), t-tests were used to test whether the slope of each regression model differed from 1, and the intercept differed from zero.

4.2.3 Time of day

Because daylength varied throughout the winter period, the time each 30-second observation period was expressed as the proportion through the period of daylight at which the observation was made. This was calculated from predicted times of civil twilight for Newbiggin-by-the-sea, Northumberland (55º 11' 15"N 1º 30' 32"W) obtained from the US Naval Observatory (Astronomical Applications Department, US Naval Observatory, Washington, DC 20392-5420, USA). Because flocks were observed for periods of up to three hours, mean observation time could not be used to express time of day directly for flock measures. The mean time of observation of the flock was therefore used to assign each flock to a division of the day. The daylight period of each day was divided into three equal phases based on this proportion, and the observations assigned to one of these phases. The phases were termed Morning (0-0.33 through the day), Midday (0.34-0.66) and Afternoon (0.67-1).

4.2.4 Environmental conditions

Real-time wind speed and temperature values were extracted from hourly UK Land Surface Station weather station data for Boulmer, Northumberland (55º 25' 0N 1º 35' 0W), obtained from the Meteorological Office via the British Atmospheric Data Centre (BADC, Space Science and Technology Department, R25 - Room 2.119, Rutherford Appleton Laboratory, Didcot, Oxfordshire, OX11 0QX, UK). Predicted sea level height was calculated for each observation of a focal bird, using tidal curves in UK Hydrographic Office tide tables (UKHO, Admiralty Way, Taunton, Somerset, TA1 2DN, UK).

4.2.5 Data analysis

Most parameters were likely to be associated with flock size in some way. All analyses therefore controlled for flock size within the SPSS statistical package using, as appropriate, partial correlations, stepwise multiple regressions, or general linear models with flock size as a covariate. The last

is equivalent to an ANCOVA where a categorical variable is used as the fixed factor. In some cases, flock ID or bird ID was entered into the model as a random factor to account for the fact that multiple measurements were taken from the same flock or individual. In Northumberland, spring low tides occur in the morning, and neap low tides in the afternoon. Because tidal cycles were superimposed non-randomly onto diurnal cycles in this way, analyses looking for diurnal patterns included the height of the tide at the time of observation and flock size as covariates.

4.3 Results

4.3.1 Inter-observer reliability

Foraging data were obtained for 764 focal birds in 44 flocks (22 flocks in intertidal habitats, 22 in supratidal habitats). The mean differences between the scores of number of pecks and head-ups made by the two observers on the 20 "training" birds were not statistically different from zero (paired t-tests, peck data: $t = 0.06$, d.f. = 19, $p = 0.956$; head-up data: $t = 0.72$, d.f. = 19, $p = 0.479$). Furthermore, regression models fitted to the peck data and head-up data indicated a high degree of correspondence between the two sets of measurements (table 4.1). Both observers' scores for the amount and polarity of aggressive encounters were identical for all 20 birds. Because of this high degree of correspondence, data from the two observers were pooled for subsequent analyses.

Table 4.1 Regressions of measurements by two observers of number of pecks and number of head-ups performed by 20 foraging ruddy turnstones in a 30-second period. In both cases, the t-tests indicate that the slopes of regression models do not differ significantly from 1 and the intercepts do not differ from zero. This indicates that there is both high between-observer repeatability and no detectable systematic bias in the dataset.

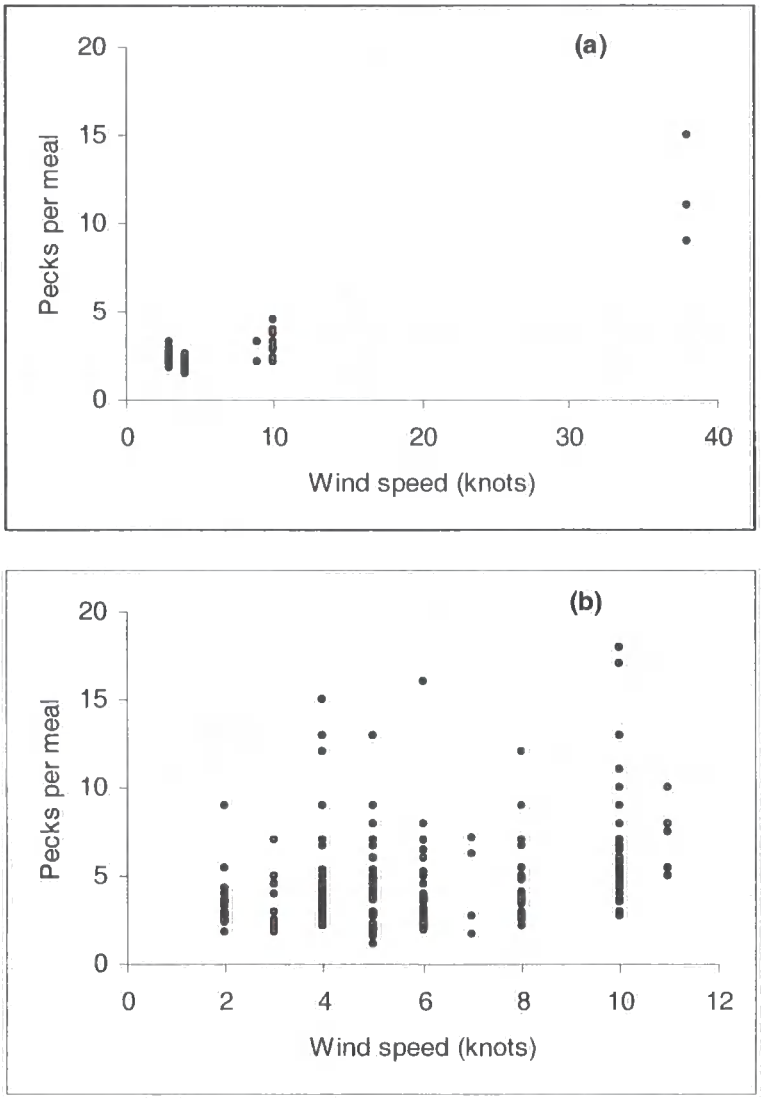
	R^2	Slope±95% CI	t	p	Intercept±95% CI	t	p
Pecks	0.84	0.87±0.27	-0.99	>0.2	3.36±7.45	0.95	>0.2
Head-ups	0.82	1.09±0.38	0.52	>0.5	0.05±0.85	0.12	>0.5

4.3.2 Weather conditions

Wind speed varied between 2 and 38 knots during the period of data collection, and temperature varied between -1.2 and 14.1 ºC. General linear models using wind speed, temperature and flock size as covariates, and foraging substrate as a fixed factor were constructed to investigate the effects of weather conditions on foraging performance. The foraging performance measures investigated were peck rate, meal acquisition rate, the number of pecks required per meal, and energy intake per unit time. Neither of the weather variables or their interaction affected peck rate (wind speed: $F_{1,316} = 1.94$, $p = 0.165$; temperature: $F_{1,316} = 0.4$, $p = 0.527$; wind speed * temperature interaction: $F_{1,316} = 1.1$, $p = 0.301$). However, birds acquired fewer meals per unit time as wind speed increased (figure 4.1; $F_{1,316} = 11.15$, $p = 0.001$), although there was no effect of temperature or the interaction between wind speed and temperature on meals acquired per unit time (temperature: $F_{1,316} = 1.19$, $p = 0.276$; wind speed * temperature interaction: $F_{1,316} = 2.37$, $p = 0.125$). Foragers needed to perform more pecks per meal acquired in windier conditions ($F_{1,316} = 13.1$, $p < 0.001$), although temperature and the interaction between wind speed and temperature had no effect on this variable (temperature: $F_{1,316} = 0.89$, $p = 0.347$; wind speed * temperature interaction: $F_{1,316} = 1.26$, $p = 0.262$). These effects of weather conditions on foraging performance meant that foragers gained less energy

per unit time while foraging in high wind speeds ($F_{1,316} = 18.8$, $p < 0.001$), low temperatures ($F_{1,316} = 5.1$, $p = 0.025$), and a combination of these factors (wind speed * temperature interaction: $F_{1,316} = 9,2$, $p = 0.003$). There was a strong effect of substrate on all four foraging performance measures, independent of flock size and weather conditions (all $F_{3,316} > 7.9$, all $p < 0.001$); this substrate effect is examined in more detail in the next section.

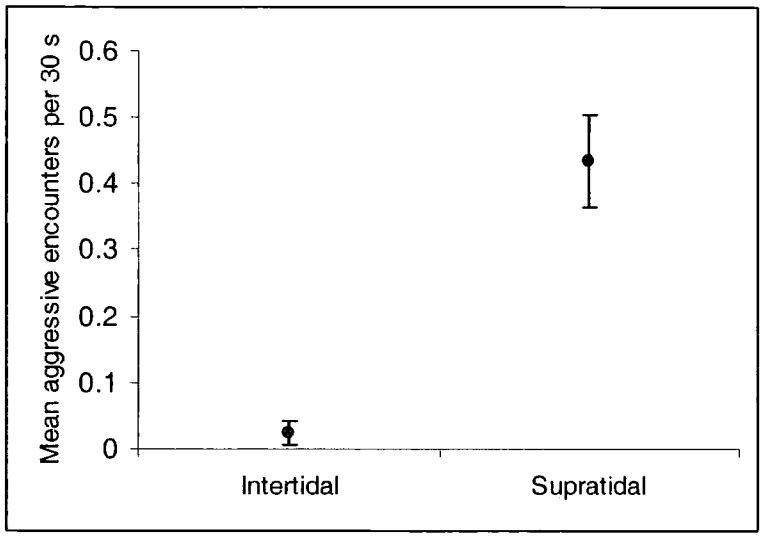
Figure 4.1 The relationship between wind speed and foraging efficiency expressed as number of pecks required to obtain a meal for (a) intertidal foragers on *Fucus*-covered rocks (r = 0.93, n = 44, p < 0.001) and (b) supratidal foragers on beach-cast wrack deposits (r = 0.36, n = 246, p < 0.001). The relationship in (a) remained significant after removal of the three points with high leverage at 38 knots (r = 0.38, n = 38, p = 0.016).



4.3.3 Comparison between flocks foraging intertidally and supratidally

Despite being available throughout the tidal cycle, habitats classified as supratidal (strandline, bare sand, beach-cast wrack) were only used during the high water period. During the low water period, observations were made on *Fucus*- and barnacle-covered rocks. Although use of habitats other than these, and use of these habitats at other tidal states was observed throughout the course of this research project, data from them were not collected for this part of the study as their use was relatively rare (see chapter 6). Flocks foraging on supratidal habitats were much larger than those on intertidal habitats (mean flock size on supratidal habitats = 18.9, on intertidal habitats = 7.2; $t = 3.1$, d.f. = 36, $p = 0.004$). Given this effect, and because flock size was likely to influence many aspects of foraging behaviour, all subsequent analyses control for flock size by including it as a covariate within a general linear model unless otherwise stated. Supratidal flocks were denser than intertidal flocks ($F_{1,35} = 22.91$, $p < 0.001$). Individuals foraging supratidally performed more head-ups than birds foraging intertidally ($F_{1,761} = 34.3$, $p < 0.001$), and were involved in more aggressive encounters (see figure 4.2; $F_{1,761} = 48.3$, $p < 0.001$).

Figure 4.2 Ruddy turnstones foraging on supratidal habitats were involved in significantly more aggressive encounters than birds foraging on intertidal habitats. Error bars are 95% confidence intervals. This difference remained highly significant after removing the effect of flock size (see text for details).

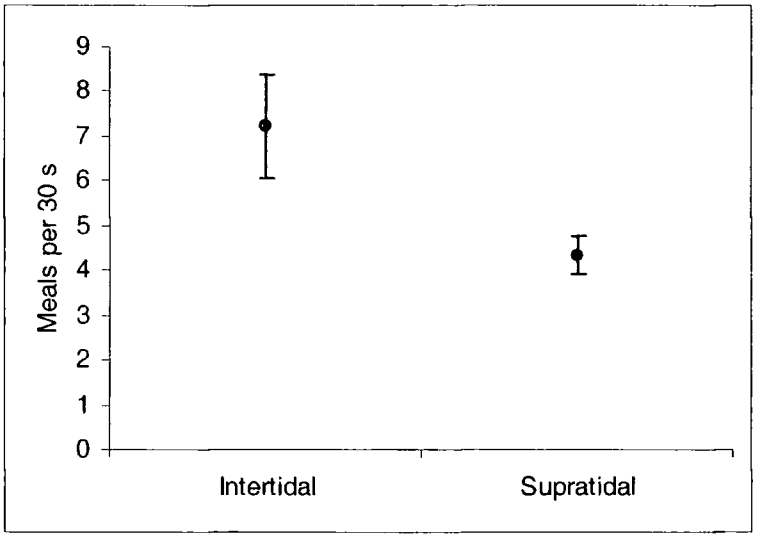


Foragers positioned centrally within beach-cast wrack foraging flocks were involved in more aggressive interactions than peripheral foragers (mean aggressive encounters for central foragers: 0.80 per 30 s; for peripheral foragers: 0.32 per 30 s; $F_{1,252} = 17.51$, $p < 0.001$). To test whether this increase in aggression was associated with an increase in vigilance (i.e. birds were using at least some head-up movements to scan for competitors), I looked at the difference between head-ups performed by central and peripheral foragers after removing the effect of flock size. There was no difference in vigilance between central and peripheral foragers on beach-cast wrack (ANCOVA: $F_{1,252} = 2.4$, $p > 0.1$). Moreover, individual vigilance on beach-cast wrack did not vary with the number of aggressive interactions the bird was involved in after the effect of flock size was removed ($F_{5,431} = 0.35$, $p > 0.8$). These results suggest strongly that the head-up posture can be interpreted overwhelmingly as vigilance for predators rather than competitors.

Peck rates did not differ significantly between intertidal and supratidal foragers ($F_{1,761} = 0.28$, $p = 0.597$), although birds acquired more meals per unit time while foraging intertidally than supratidally (figure 4.3; $F_{1,333} = 29.65$,

$p < 0.001$). Consequently, intertidal foragers performed a mean of 3.4 pecks per meal, while supratidal foragers performed 4.8 pecks per meal. This difference was highly significant ($F_{1,321} = 26.26$, $p < 0.001$).

Figure 4.3 Foragers ingested meals at a significantly faster rate on intertidal versus supratidal habitats. The mean intake rate on intertidal habitats was 7.23 meals per 30 s, while on supratidal habitats it was 4.34 meals per 30 s. Error bars represent 95% confidence intervals.



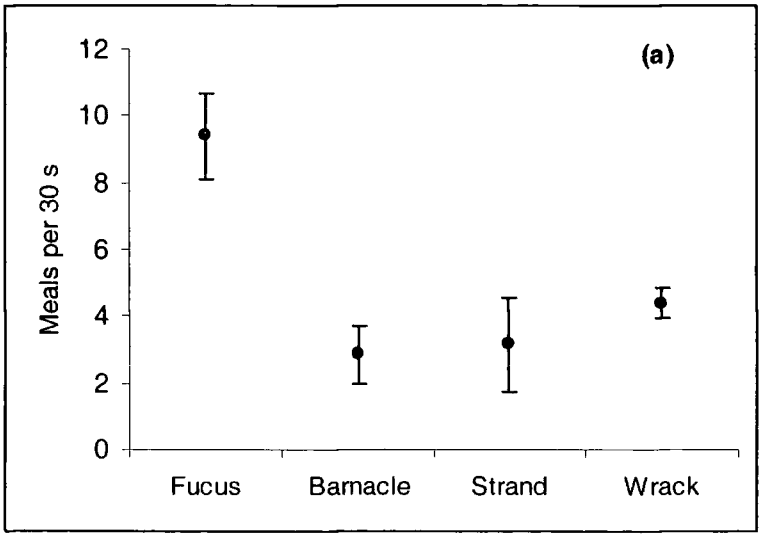
4.3.4 Substrate and foraging efficiency

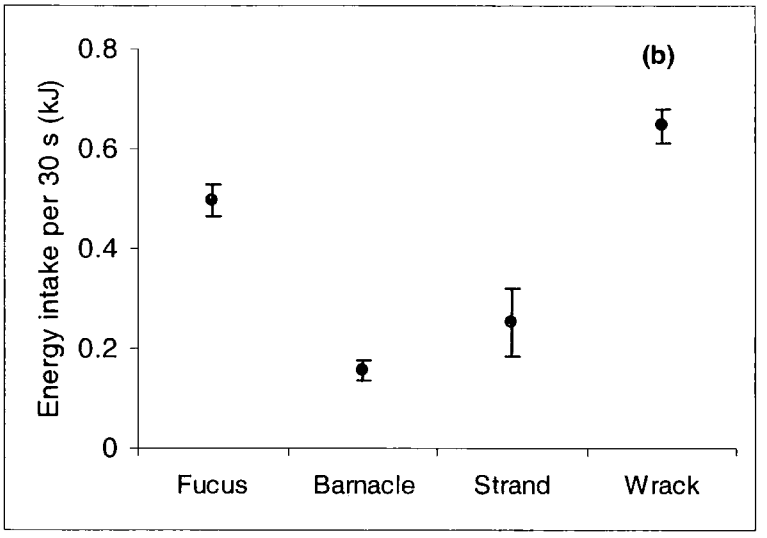
Peck rate did not vary with substrate (ANCOVA: $F_{5,754} = 0.74$, $p = 0.591$), suggesting that foraging effort remained relatively constant among substrates. However, foragers needed to perform significantly fewer pecks per meal obtained on *Fucus*-covered rocks than all other substrates (ANCOVA: $F_{3,319} = 10.31$, $p < 0.001$). This result could possibly have been due to birds with poorer foraging efficiency going on to feed supratidally, leading to an underestimate of general foraging efficiency on supratidal habitats. This did not appear to be the case, however, because all three marked individuals where sufficient data existed made fewer pecks per meal foraging intertidally on *Fucus*-covered rocks than they did supratidally foraging on beach-cast wrack (Ring number SX83525, $t = 3.42$, d.f. = 18,

p = 0.003; SX83099, t = 3.6, d.f. = 13, p = 0.003; SX83524, t = 3.78, d.f. = 11.8, p = 0.002).

Foragers obtained significantly more meals per unit time on *Fucus*-covered rocks than all other substrates (figure 4.4 (a); ANCOVA: $F_{3,331} = 8.69$, $p < 0.001$). Despite this, energy intake (see chapter 2 for calculations of energy values) was significantly higher on beach-cast wrack than other substrates, independent of flock size (figure 4.4 (b); $F_{3,333} = 16.26$, $p < 0.001$). The higher energetic content of prey items taken while foraging on beach-cast wrack therefore offset the decreased rate of meal acquisition on beach-cast wrack. To check for density dependence on supratidal substrates, flock density was correlated with energy intake. The correlation coefficient describing the relationship between the two variables, although indicative of only a weak relationship, was in fact positive (r = 0.19, n = 259, p = 0.002), suggesting that energy intake was more dependent on substrate quality than density of foragers.

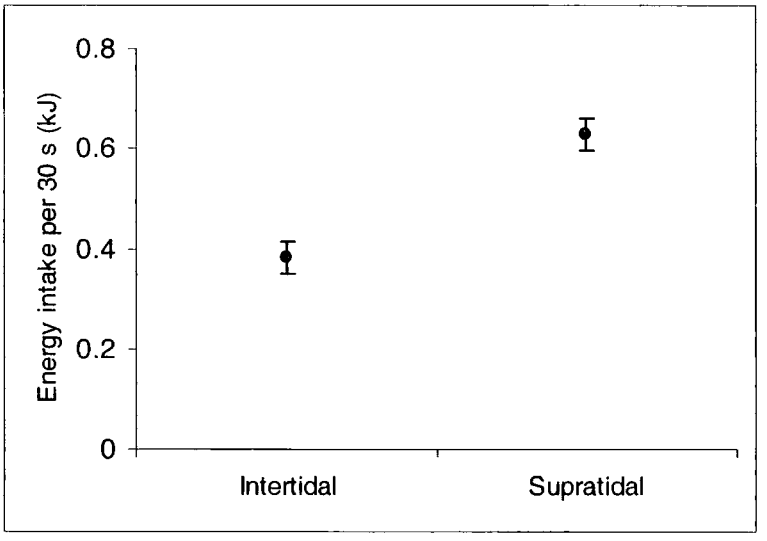
Figure 4.4 (a) Foraging success per unit time on different foraging substrates. The only significant comparisons were between *Fucus*-covered rocks and the other three substrates (pairwise ANCOVAs; all $p < 0.001$). (b) Energy intake per unit time for a constantly feeding bird on the same four substrates. The high energy content of coelopid fly larvae meant that energy intake per unit time was higher on beach-cast wrack than other substrates. Error bars are ± 1 SE.





These substrate effects translated into a significantly higher energy intake rate for foragers on supratidal habitats than for foragers on intertidal habitats, independent of flock size (figure 4.5; $F_{1,321} = 23.6$, $p < 0.001$).

Figure 4.5 Energy intake rate for a constanly feeding bird was much higher for foragers on supratidal habitats than intertidal habitats. Error bars are 95% confidence intervals.



4.3.5 The group size effect

An ANCOVA using flock size as a covariate, rate of head-ups as the dependent variable, and substrate as a fixed factor confirmed the presence of a negative relationship between flock size and individual vigilance rate ($F_{1,727} = 45.8$, $p < 0.001$). Furthermore, there was a highly significant overall effect of substrate on the group size effect ($F_{3,727} = 38.41$, $p < 0.001$). Pairwise ANCOVAs including flock size as a covariate supported the three general predictions made above. Foragers on supratidal habitats initiated vigilance postures at a significantly higher rate than those on intertidal habitats ($F_{1,761} = 34.32$, $p < 0.001$). Within intertidal habitats, foragers on barnacle-covered rocks initiated vigilance postures at a significantly higher rate than those on *Fucus*-covered rocks ($F_{1,216} = 4.05$, $p = 0.045$). Within supratidal habitats, foragers on beach-cast wrack initiated vigilance postures at a significantly higher rate than those on strandline habitats ($F_{1,510}$, $p < 0.001$). These results indicate that foragers on more risky habitats were increasing their individual vigilance levels above that predicted by the group size effect alone.

After discovering these effects on individual vigilance, flock-level vigilance was investigated using interscan interval, the estimated gap in seconds between the initiation of a head-up by any one flock member. After controlling for the effect of flock size, interscan interval varied significantly among the four substrate types (ANCOVA: $F_{3,31} = 6.1$, $p = 0.002$). Subsequent pairwise comparisons showed that interscan interval was greater on intertidal habitats than supratidal habitats ($F_{1,34} = 6.96$, $p = 0.012$). Furthermore, within supratidal habitats, interscan interval was greater on strandline debris near the shoreline than on beach-cast wrack, situated further up the shore ($F_{1,16} = 7.58$, $p = 0.014$). Within intertidal habitats, no difference could be detected in interscan interval between *Fucus*-covered rocks and barnacle-covered rocks ($F_{1,14} = 0.49$, $p = 0.494$). These results indicate that vigilance by flocks foraging supratidally was greater than predicted by flock size alone, and further that birds were most alert on beach-cast wrack as opposed to other supratidal habitats.

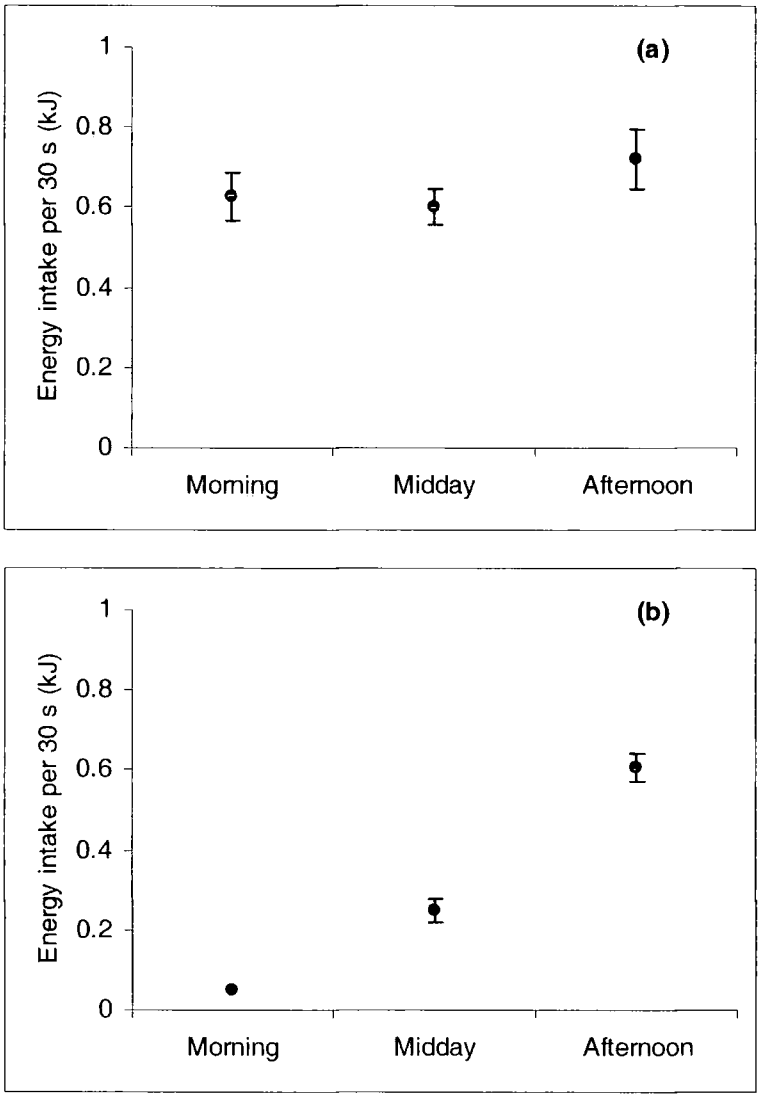
In flocks feeding on beach-cast wrack, the number of head-ups performed by individual birds declined with flock size. Flock density had no separate effect, as it was excluded from a stepwise multiple regression model initially including flock size and flock density (final model: $F_{1,436} = 31.43$, $p < 0.001$). This was because flock size and density were positively correlated ($r = 0.44$, $n = 730$, $p < 0.001$). The change in head-up rate appeared to be driven by a changing need for predator vigilance rather than as a result of increased competition for resources, as the number of aggressive encounters by individuals did not vary with flock density ($r = 0.06$, $n = 438$, $p = 0.189$), and was uncorrelated with vigilance ($r = -0.001$, $n = 438$, $p = 0.977$).

4.3.6 Diurnal patterns in foraging behaviour

The size of flocks foraging supratidally was significantly higher in the morning and afternoon periods than in the midday period (one-way ANOVA: $F_{2,512} = 38.36$, $p < 0.001$). Therefore, as with previous analyses, all tests for diurnal patterns controlled for flock size by including it as a covariate. As explained above, these analyses also control for tide height at time of observation by including it as a covariate within a general linear model.

Energy intake rate by individuals foraging supratidally remained unchanged during the course of the day (figure 4.6 (a); ANCOVA: $F_{2,265} = 0.10$, $p = 0.904$). For birds foraging intertidally, however, there was a significant increase in energy intake rate throughout the day (figure 4.6 (b); $F_{2,63} = 25.93$, $p < 0.001$).

Figure 4.6 The diurnal pattern in individual energy intake rate for ruddy turnstones feeding (a) supratidally and (b) intertidally. Values are the mean number of meals ingested by foraging birds in 30-second observation periods. Error bars are ± 1 SE. For supratidal foragers, no comparisons were significant (pairwise ANCOVAs; all $p>0.05$). For intertidal foragers, the comparison between the midday and afternoon periods was significant ($F_{1,62} = 34.9$, $p < 0.001$). Data were collected for only one individual foraging intertidally in the morning period, so error could not be estimated.



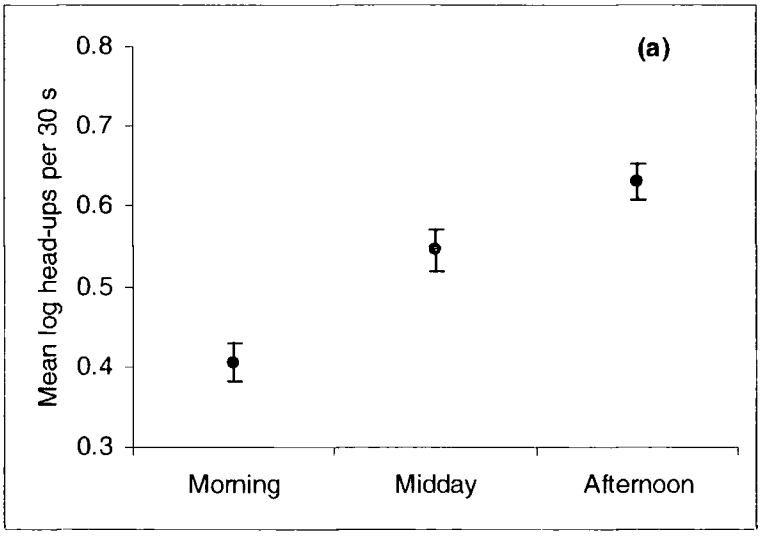
The number of pecks a forager performed on beach-cast wrack to obtain a meal changed significantly through the course of the day (GLM using flock size and tide height as covariates, and day division as a fixed factor: $F_{2,241} = 3.42$, $p = 0.034$). Subsequent pairwise ANCOVAs indicated that foragers performed more pecks per meal in the morning and afternoon

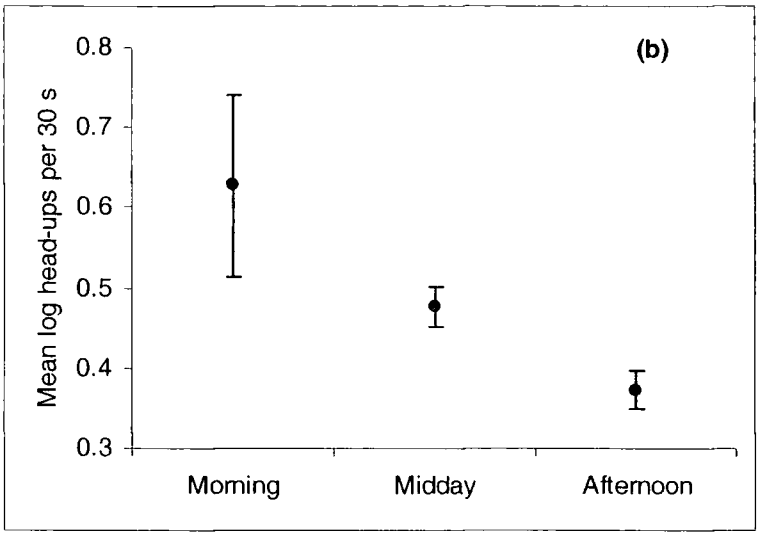
periods than in the midday period (morning versus midday period: $F_{1,201}$ = 9.7, p = 0.002; midday versus afternoon period: $F_{1,157}$ = 11.57, p = 0.001).

4.3.7 Diurnal patterns in vigilance behaviour

The mean number of head-ups performed by individuals foraging supratidally changed significantly during the course of the day, after controlling for the effects of flock size and tide height ($F_{2,510}$ = 7.47, p < 0.001); it increased between the morning and midday, and midday and afternoon periods (figure 4.7 (a)). For birds foraging intertidally, however, individual vigilance declined throughout the day, although the overall effect was weaker ($F_{2,244}$ = 3.25, p < 0.05), and the only significant difference was between the midday and afternoon periods (figure 4.7 (b)).

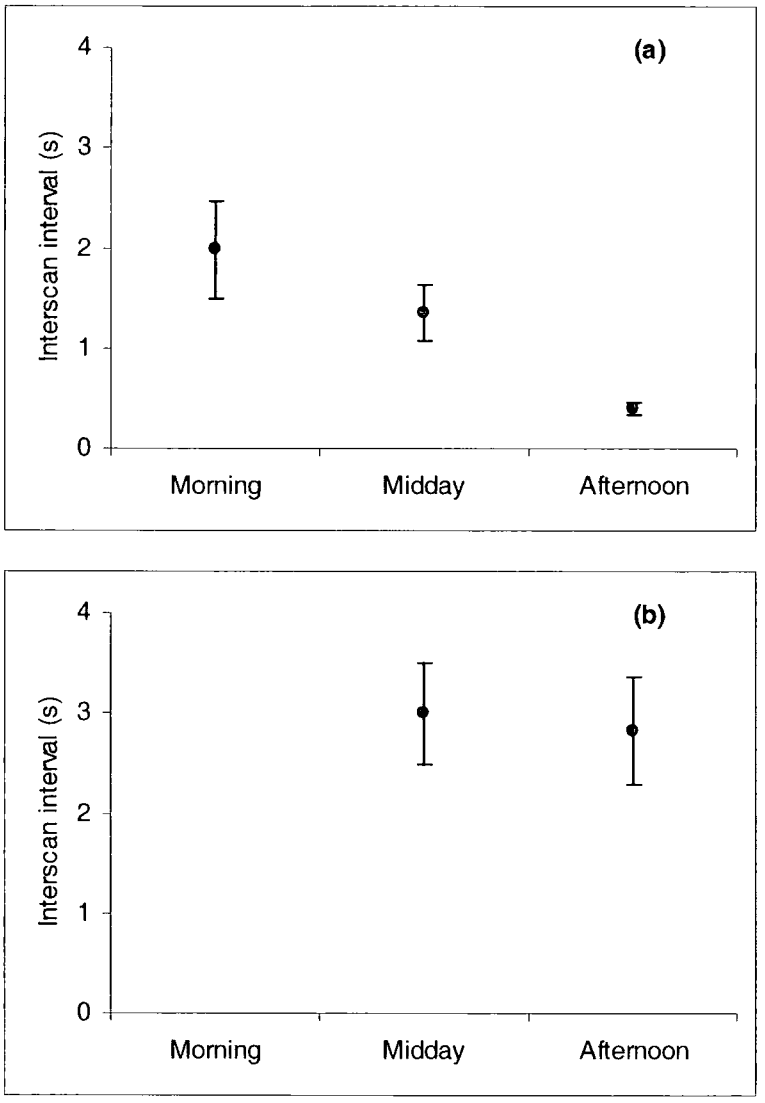
Figure 4.7 The diurnal pattern in individual vigilance for ruddy turnstones feeding (a) supratidally and (b) intertidally. Values are the mean log head-ups performed by individuals in 30-second observation periods. Error bars are ± 1 SE. For supratidal foragers, all comparisons were significant (pairwise ANCOVAs; all p < 0.05). For intertidal foragers, only the comparison between the midday and afternoon periods was significant (pairwise ANCOVA: $F_{1,242}$ = 6.14, p = 0.014).





To assess whether these individual effects translated into flock-level effects, change in flock interscan interval was also investigated in relation to time of day. In flocks foraging supratidally, interscan interval differed strongly between divisions of the day, after controlling for flock size and tide height (figure 4.8 (a); $F_{2,15} = 9.0$, $p = 0.003$), declining significantly between the morning and afternoon periods, and between the midday and afternoon periods. For intertidal flocks, there was no difference in interscan interval between the midday and afternoon periods (figure 4.8 (b); $F_{1,15} = 0.39$, $p = 0.540$). No intertidal flock observations could be assigned to the morning period, although some individual observations were made during that time. This was because the mean time of observation of the whole flock was used to calculate flock measures (see section 4.2.3). No mean time of observation of a whole flock fell within the morning period.

Figure 4.8 The diurnal pattern in flock vigilance for ruddy turnstone flocks feeding (a) supratidally and (b) intertidally. Interscan interval is the estimated time in seconds between successive initiations of the head-up posture by any one flock member. Error bars are ± 1 SE. The significant comparison for the supratidal data was between morning and afternoon (pairwise ANCOVA: $F_{1,10} = 18.37$, $p = 0.002$), although the midday and afternoon comparison approached significance (pairwise ANCOVA: $F_{1,9} = 3.72$, $p = 0.086$).



4.4 Discussion

This study has demonstrated significant differences in vigilance, group size, and various foraging parameters among alternative foraging substrates. Foragers generally gained more energy per unit time, and showed higher vigilance levels on supratidal substrates than on intertidal substrates, which were also the substrates predicted to be subject to increased predation risk. Considering all substrates together, individual vigilance rate declined with increasing flock size as predicted by the group size effect, although there was some scatter in the relationship. Much of this scatter was explained by variation in predation risk among the habitats; birds were more vigilant than predicted by the group size effect in habitats in which a higher likelihood of attack by a raptor was predicted. These results provide much needed field-based evidence that variation in predation risk confounds the group size effect (Roberts 1995, 1996, Lima & Bednekoff 1999b).

This study has also demonstrated significant diurnal patterns in energy intake rate and vigilance contribution for ruddy turnstones. Foragers on profitable, but predation-risky and ephemeral habitats showed a consistently high level of energy intake through the day, predicting monotonic mass gain, and vigilance increased through the day, as foragers neared satiation and the risk of mass-dependent predation increased. Foragers on poorer quality, but relatively predation-safe and less ephemeral habitats delayed energy intake until late in the day, and decreased vigilance as the day progressed, directly trading off foraging effort and vigilance. These patterns generally agree with predictions arising from state-dependent foraging models.

4.4.1 Predation risk and the group size effect

The head-up posture performed by ruddy turnstones as defined here appeared to have the primary function of scanning for predators, rather than monitoring conspecifics or searching for prey items or foraging areas. This suggests that the rate of head-ups performed by a forager was a good

measure of anti-predator vigilance and that we can use it to study changes in perceived predation risk by foragers, and look for ways in which foragers integrate information on group size and predation risk.

Foragers formed larger flocks in supratidal than intertidal habitats. Some of this effect may have arisen from the patchiness of supratidal feeding resources, but the fact that individuals foraging supratidally were more vigilant than intertidal foragers, despite the fact they were forming larger flocks suggests very strongly that the birds were, at least in part, responding to changes in perceived predation risk. This response had three stages.

Firstly, supratidal foragers formed larger flocks, thereby reducing individual predation risk through the effects of dilution (Foster & Treherne 1981), predator confusion (Milinski 1979b) and cooperative warning and escape effort (Humphries & Driver 1967, Proctor et al. 2003). This also meant that the vigilance burden could be shared among more individuals.

Secondly, the increase in flock size allowed individuals to reduce their own vigilance contribution, and there was an overall negative relationship between group size and individual vigilance. This effect translated into a flock effect, whereby interscan interval measured across the whole flock was also adjusted to flock size. The most frequently used supratidal foraging substrate was beach-cast wrack (see chapter 6). Given that this substrate is highly profitable, it is perhaps not surprising that no density-dependent depression in energy intake rate was found (Goss-Custard et al. 1992). It is likely that the high invertebrate numbers within beach-cast wrack deposits meant that ruddy turnstone flocks did not reach sufficient density to deplete stocks, and forager densities were not sufficiently high to cause direct interference (Houston & Lang 1998, Parker & Sutherland 1986, van der Meer 1997). This lack of density dependence suggests that ruddy turnstones on supratidal substrates will always do better in larger flocks. It also suggests that models of supratidal feeding need not include density dependent effects (i.e. the bird being less likely to feed supratidally if many others have made the same decision), only individual condition, and patch quality measures.

Thirdly, individuals moderated their reduction in individual vigilance to allow for the fact that the likelihood of a predator attacking the flock had increased. Birds were therefore more vigilant than predicted from the general group size effect. This suggests that foragers can integrate predation risk and group size information when making decisions about their vigilance contribution. Although foragers did form larger flocks on beach-cast wrack, these were not large enough to bring group vigilance up to the necessary level in response to the increase in predation risk.

In common with many studies (see reviews in Barnard & Thompson 1985, Elgar 1989, Lima & Dill 1990, Roberts 1995), this study has detected an effect of group size on vigilance. However, using data from unmanipulated field conditions, it has shown that the relationship between individual- and flock-level vigilance and group size varies according to predation risk. Foragers in risky situations show greater vigilance than predicted by the flock size effect alone. It has been shown that the vigilance of starlings *Sturnus vulgaris* foraging on the periphery of flocks declines more slowly with flock size than the vigilance of birds foraging centrally, and this was attributed to variation in predation risk (Jennings & Evans 1980), although not interpreted in the sense of affecting the nature of the group size effect. This study therefore adds another variable to the growing list of confounders of the group size effect (Roberts 1996, Treves 2000, Beauchamp 2001).

Lima & Bednekoff (1999b) recently extended Houston & McNamara's (1993) model to include alternative scenarios of temporal change in risk to foragers, and demonstrated that anti-predator behaviour must reflect the pattern of change in risk, not just the fact that risk changes. It would be interesting to look at the differences in risk-management strategies between the different high water feeding strategists. Lima & Bednekoff (1999b) predict that where high risk situations are rare, foragers should show the greatest anti-predator behaviour in that high risk situation, and that this must necessarily decline as high risk situations become commoner. This study system presents an ideal opportunity to test this hypothesis empirically. The model of Lima &

Bednekoff (1999b) predicts that average vigilance on supratidal substrates should decline as the propensity of an individual to feed supratidally increases.

Although the effect in this system is strong because the habitats differ significantly both in profitability and predation risk, these parameters may vary much more subtly in other systems, and confound the group size effect. Field studies using the group size effect would need to identify and control for variation in both profitability and predation risk among alternative foraging areas, whether or not these are immediately obvious to the human investigator.

4.4.2 Diurnal patterns in vigilance and energy intake

All diurnal patterns identified during this study occurred independently of changes in flock size. Furthermore, they were independent of changes in sea level height at the time of each observation, indicating that the fact that spring low tides always occurred in the morning period did not affect the results. Foragers formed larger flocks in the morning and afternoon periods than during the midday period. This could be in response to elevated predation risk at these periods of the day. It has been shown that vigilance during early morning foraging by dark-eyed juncos *Junco hyemalis* is influenced by perceived predation risk, in particular the brightness of available light (Lima 1988b). Starting to forage too early in the morning could increase predation risk, and starting too late could increase starvation risk (Lima 1988a). Forming larger flocks early and late in the day could allow foragers to minimise their risk of predation while also minimising their own vigilance contribution at a time when energy reserves are low through overnight metabolism in the former case, and through the need to store reserves for the next overnight period in the latter case.

Energy intake and vigilance showed distinct diurnal patterns, independent of flock size. Early in the day, foragers on supratidal habitats (unpredictable, profitable, risky) showed low levels of vigilance. Presumably, it is worth a

forager taking the risk with an unpredictable but profitable resource early in the day if it has access to a patch. McNamara et al. (1994) predicted that on high profit substrates, foragers would show a bimodal pattern of mass gain. The results of this study suggest that where the high profit substrate is also risky and unpredictable, foragers may be prepared to take the extra predation risk early in the day, and then increase vigilance levels as the day progresses and satiation and mass-dependent predation take effect, thereby by producing a single peak of mass gain early in the day. As the forager puts on weight through the day, starvation becomes less likely and it should be prepared to accept less risk. However, given that the resource is unpredictable, it is worth continuing to forage at a high rate if the forager still has access to a patch, accepting this elevated mass-dependent predation risk later in the day (Bednekoff & Houston 1994).

It is surprising that vigilance and energy intake did not show mirrored relationships for supratidal foragers i.e. there did not appear to be a direct trade-off between intake rate and vigilance. However, the number of pecks a forager performed to obtain a meal was significantly lower in the midday period than in the morning or afternoon periods, so it is possible that changes in selectivity were occurring during the course of the day that were being masked by the approach of using mean prey energy value to obtain energy intake values based on the number of meals ingested. The possibility of diurnal changes in selectivity by ruddy turnstones requires further investigation. However, as a bird nears satiation, there is no reason why it should reduce foraging effort, but there are good reasons why it should be increasingly vigilant as the immediate risk to survival is influenced far more by predation risk than by starvation. A decrease in selectivity could be a price worth paying under such circumstances. Another possible complicating factor here is that birds not exhibiting a head-up posture may still be vigilant to some degree (Lima & Bednekoff 1999a), and presumably this "head-down" vigilance effort may vary with physiological state and time of day. This would be an interesting avenue for further study, including the effects of "head-down" vigilance on the efficiency and selectivity of foragers.

In intertidal habitats, characterised by low profitability and predation risk, but high predictability, foragers appeared to trade off vigilance and feeding much more directly. Vigilance declined through the day, whereas energy intake increased. When using a predictable resource, the forager has control over when to achieve energy intake. Where there is no possibility of escape to predation-free areas (Bednekoff & Houston 1994, McNamara et al. 1994), it makes sense to delay weight gain until late in the day to minimise mass-dependent predation risk. As foraging effort increases during the course of the day, foragers are increasingly constrained from devoting time to vigilance behaviours (Dimond & Lazarus 1974, Caraco 1979, Mooring & Hart 1995). In sum, these results present field evidence to support predictions that foragers dynamically adjust diurnal patterns of foraging and vigilance to resource characteristics such as predictability, profitability and predation risk (Lima & Bednekoff 1999b).

4.4.3 Vigilance and aggression in supratidal flocks

Aggression by supratidal foragers was not strongly density-dependent or related to vigilance or energy intake rate, although it did change with position in the flock. Unlike in some other cases, this study did not detect an effect of position within the flock on vigilance levels. Several studies have shown that peripheral foragers show elevated vigilance levels compared to central foragers (Hamilton 1971, Petit & Bildstein 1987, Dominguez 2003; although the last study did not control for flock size), and some have interpreted this in terms of elevated predation risk for peripheral foragers (Hamilton 1971, Jennings & Evans 1980). In the current study system, there is unlikely to be a large differential in predation risk across the flock. Mean flock diameter was only 6 m, and because supratidal feeders are likely to be attacked from above, predation risk is likely to be relatively uniform across the flock. This remains to be tested, particularly as absolute position up the shore will vary with position in the flock. The main effect of position in the flock in this study was on aggression levels, with central foragers engaging in more aggressive encounters than peripheral foragers. The elevated aggression levels associated with supratidal feeding, and particularly those in the centre of

supratidal feeding flocks, may play a social role, such as reinforcement, rather than simply being associated with high flock density. Again, this requires further investigation.

4.4.4 Conclusion

This part of the study has shown that foragers respond to variation in predation risk by forming larger flocks and then by adjusting their vigilance levels in a more subtle way than predicted by the group size effect alone. Furthermore, individuals alter their diurnal patterns of foraging and vigilance in the way that predictions arising from differentials in predation risk resource quality and resource predictability would suggest. The next stage is to tease apart in a field setting the effects of resource quality, predictability and probability of attack by a predator. The ruddy turnstone / beach-cast wrack system presents an ideal opportunity to achieve this. Given suitable resources, experimental manipulation of the quality and predictability of beach-cast wrack deposits could be achieved in a field setting, and variation in attack likelihood could be simulated.

Chapter 5: Spatial associations between ruddy turnstones and their food resources

5.1 Introduction

Resources available to foragers vary both spatially and temporally. The responses of foragers to this variation have been extensively modelled (Andersson 1978, 1981, McNair 1982, Lessells & Stephens 1983, Roche 1996). Where potential food is distributed patchily through the environment, higher prey densities or more profitable prey types compensate for greater travel costs associated with visiting specific patches. If prey capture rate falls below a threshold level (theoretically the average prey capture rate across all possible patches), a forager should abandon the current patch and move to a new one (Charnov 1976). The time spent resident in a patch will therefore increase with prey density in that patch, particularly where a patch is highly profitable relative to other available patches. Because it is worth paying a higher cost of transport to get to a profitable patch, we might expect concentrations of foragers that have travelled varying distances in profitable patches and spatial tracking of profitable resource patches, particularly where foragers do not have to take food back to a central location such as a nest. Indeed, it has been shown experimentally that foragers spend a large proportion of their time in regions of highest prey density (Smith & Dawkins 1971).

Despite much theoretical (Oaten 1977, Green 1984, McNamara & Houston 1980, Ollason 1980, Clark & Mangel 1984) and experimental (Krebs et al. 1977, Ydenberg 1984, Tamm 1987, Naef-Daenzer 2000) support for these predictions, the distributions of foragers under natural conditions frequently cannot be predicted by this marginal value approach (Valone 1991, Valone & Giraldeau 1993, Alonso et al. 1995). For example, the costs of movement may vary among individuals in a population, particularly in social foragers. This might limit the degree to which a forager can track profitable patches across space. I studied spatial tracking of a highly profitable resource in a

non-breeding shorebird. Ruddy turnstones are generally highly site faithful within and between years, but the distribution of home range sizes is positively skewed (Metcalfe & Furness 1985, Metcalfe 1986), indicating that there is continuous individual variation in spatial ranging behaviour. I wanted to know whether this variation was associated with spatial tracking of a profitable resource, namely beach-cast wrack (see chapter 3).

Ruddy turnstones typically forage on relatively poor habitats during the low water period, while some individuals go on to feed on relatively rich, but patchy and ephemeral supratidal resources during the high water period. The appearance of beach-cast wrack deposits is spatially predictable, but highly uncertain temporally (chapter 3). Consequently, foragers could predict where, but not necessarily when, patches will become available. We might therefore expect a close spatial association between sites that regularly hold beach-cast wrack, and the locations of individual foraging ruddy turnstones. Indeed, it has been suggested that ruddy turnstones make excursive movements outwith their usual home range specifically to take advantage of deposits of beach-cast wrack, and that this might develop to such an extent that some individuals successively occupy multiple range cores in response to the appearance of beach-cast wrack (Eaton 2001).

However, it is possible that individuals might range more widely to avoid having to feed supratidally, an activity that appears to incur elevated predation risk (see chapter 4). In this chapter, I formally distinguish these two possibilities and test the predictions arising from them by measuring the propensity of individuals to feed on supratidal habitats and relating this to range size, the degree of association with supratidal habitats, and other aspects of ranging behaviour.

5.1.1 Hypotheses to explain variation in ranging behaviour by ruddy turnstones

(a) The avoidance hypothesis

Perceived predation risk appears to be higher on supratidal habitats than on intertidal habitats (see chapter 4), and the fact that foragers use them only when energy intake during the low water period has been inadequate (see chapter 6) suggests there is a cost to foraging supratidally. This cost would therefore be minimised if birds completely avoided using supratidal habitats. Birds adopting this approach would need to range more widely on intertidal habitats to locate the most profitable patches. The avoidance hypothesis therefore states that individuals range more widely to track variation in intertidal habitat quality, thus minimising the need to feed supratidally.

This hypothesis predicts a negative relationship between the propensity to feed supratidally and both range size and the degree of patchiness within a range. It also predicts that birds will feed intertidally, and to a lesser extent supratidally, during excursive movements. Intertidal and supratidal range sizes will therefore be approximately equal, because the trips are not specifically made to track the availability of supratidal resources, but rather to track long term changes in intertidal food availability. Some supratidal foraging will almost certainly be necessary even for "avoiders" over the long time scales I am considering here. Perhaps most importantly, the avoidance hypothesis predicts a negative relationship between range size and the degree of spatial association between bird locations and sites that regularly hold beach-cast wrack. This is because the motivation for ranging more widely is to sample and track variation in intertidal habitat quality, and there is no reason to expect intertidal and supratidal habitat profitability to covary spatially.

(b) The tracking hypothesis

Because supratidal habitats contain higher densities of more profitable prey types than intertidal habitats (chapter 2), starvation risk would be minimised by utilising supratidal patches frequently. This preference for supratidal habitats means that birds adopting this approach would need to track spatially the appearance of beach-cast wrack deposits. The tracking hypothesis therefore states that individuals range more widely to track variation in supratidal habitat quality, thus minimising their risk of starvation by allocating more time to feeding on profitable habitats. This hypothesis predicts a positive relationship between the propensity to feed supratidally and both range size and the degree of patchiness within a range. It also predicts that birds will feed supratidally almost exclusively during excursive movements, and that supratidal ranges will be larger than intertidal ranges, because the trips are made specifically made to track the availability of supratidal resources. Furthermore, the tracking hypothesis predicts a positive relationship between range size and the degree of spatial association between bird locations and sites that regularly hold beach-cast wrack. This is because the motivation for having a large range is to sample and track variation in supratidal habitat quality.

Here I use data collected as part of a long-term study (seven seasons to date) over a relatively large geographic area (39.5 km of rocky coastline in north-east England; see chapter 1) to investigate ranging behaviour of ruddy turnstones, and relate this to supratidal feeding parameters. The large geographic area covered by this dataset meant that, unlike many studies in shorebird ranging behaviour, substantial excursive movements by individuals could be identified. The aims of this chapter are twofold; firstly to determine whether foragers tracked spatially the appearance of supratidal foraging habitats, and secondly to investigate how the degree of spatial association varied with range size and structure. These data will allow the two hypotheses explaining variation in ranging behaviour to be distinguished.

5.2 Methods

5.2.1 Sightings of colour-marked birds

This chapter is based on sightings made between 10 February 1997 and 10 November 2002 of ruddy turnstones marked with unique colour-ring combinations[1]. The study site was a 39.5 km stretch of the Northumberland coast in north-east England (see chapter 1 for details of the study area, and appendix 1 for full details of how resightings were collected). Sightings were only included where the observer had a good view of the colour-rings and was confident of the bird's identity. Where necessary, colour-ring combinations were read with the aid of a 20-60x Optolyth telescope. Additional sightings were received from members of the public, although non-existent colour-ring combinations were rather frequent in these reports. Rather than attempt to screen the sightings, for example by deleting "unlikely" records, all data from members of public were excluded from the current analysis to avoid introducing any bias.

The location of each bird was recorded to the nearest 20 metres by reference to a grid overlaid on 1:10,000 Ordnance Survey maps of the study area. The activity of each bird was recorded as feeding or roosting. Other behaviours were not recorded for the purposes of this part of the study. Successive sightings were separated by a minimum interval of one hour. Substrate was also recorded, and categorised into intertidal and supratidal habitats. Habitats above the most recent high water mark, and / or comprising beach-cast material, were considered supratidal. Intertidal habitats comprised *Fucus*-covered rocks, bare rocks, barnacle-covered rocks, mussel-covered rocks and bare sand. Supratidal habitats comprised beach-cast wrack, strand, bare sand, fields and artificial structures. See chapter 1 for definitions strand and beach-cast wrack substrates.

[1] Sightings were made by M. Eaton until 28 March 1999 and by R. Fuller after 4 October 1999

5.2.2 Manipulating the dataset

Birds with 10 or fewer fixes (the home range measures employed below require more than 10 samples for stability (Kenward & Hodder 1996)) were excluded from further analyses. To avoid confusing the analyses with migrant individuals, sightings made between April and September inclusive were also removed from the dataset. It was possible that trimming the dataset by removing birds seen on only a few occasions could have biased the sample toward birds that only fed infrequently in supratidal habitats, because there were relatively few sites where birds fed supratidally compared to intertidally, making detecting the presence of any one bird easier. To check for this, I related the proportion of the fixes for each bird that were on supratidal habitats to the total number of sightings of that bird. Despite the large sample size, there was no significant relationship between the two variables ($r = -0.1$, $n = 227$, $p = 0.064$). This suggests that higher detectability of birds feeding supratidally did not bias the dataset, and that selecting only winter records and birds with more than 10 fixes did not introduce further bias into the dataset.

5.2.3 Estimating individual ranging behaviour

Many methods have been used to describe empirically the home ranges of animals (White & Garrott 1990), and evaluations of the performance of various methods have formed entire studies in themselves (Spencer & Barrett 1984, Worton 1989b, Harris et al. 1990, Seaman & Powell 1996). The choice of method ultimately depends on the questions being asked. To describe spatial associations between ruddy turnstones and their foraging resources, I am asking questions about the maximum extent of individual ranging behaviour, the typical extent of individual ranging behaviour, and the degree of spatial variation in an individual's location, in other words patchiness of space use within the range. Each of these questions requires different spatial analysis techniques.

One of the best ways to measure the maximum extent of an individual's ranging behaviour is to construct a minimum convex polygon around all locations for that individual (White & Garrott 1990). Although the area and shape of the minimum convex polygon is heavily influenced by outlying fixes (Harris et al. 1990), it is the most objective way to measure the total area used by animals. Given that intertidal habitats in the study area were arrayed broadly linearly, a further measure, range span, was used to express total range of movement by the birds. Range span is simply the distance along the longest axis of the range of each bird.

It is unlikely that the birds will use all areas within the minimum convex polygon equally. Although ruddy turnstones have relatively stable home range cores both within and between winters, they are also known to make excursive trips from these range cores (Burton & Evans 1997, Eaton 2001), so there is a need for a measure of the typical extent of individual ranging behaviour. For any location within an individual's home range there is an associated probability of encountering the animal at that point (Jennrich & Turner 1969, Anderson 1982, Worton 1989a). Kernel analyses identify regions of high usage by estimating the pattern of fix density across a range (Dixon & Chapman 1980, Spencer & Barret 1984, Worton 1989a). They are relatively unbiased by small sample sizes (Worton 1989a). An arbitrary grid is placed across the range, and fix densities are derived at intersections of the grid using a bivariate normal kernel estimator. Contours containing a specified percentage of the fixes are then interpolated across the grid and polygons constructed (Kenward & Hodder 1996). To reduce the influence of extreme outliers, the usual method is to exclude the 5% of the fixes furthest from the harmonic mean centre (Bekoff & Mech 1984, Harris et al. 1990, White & Garrott 1990), and this was the approach adopted here.

While kernel analysis is useful for identifying areas of typical usage within a range, the technique best suited to identifying patchiness in range use, for example where individuals forage in several separate areas, is cluster analysis (Kenward & Hodder 1996). The technique begins by identifying the two fixes that are closest together and have the nearest third fix. The polygon

enclosing these points becomes the first cluster. Providing there is no other potential new cluster in which the distance to the third fix is shorter, the fix closest to the existing cluster is added to the cluster. If another potential cluster has a shorter distance to its third fix, that new cluster is formed. If the fix nearest any cluster is already assigned to another cluster, the two clusters join. When all fixes have been assigned to clusters, a minimum convex polygon is drawn around each cluster and its area calculated (Kenward 2000).

5.2.4 Home range measurements

For spatial analyses, the locations of bird fixes (both feeding and roosting records) were converted into co-ordinates on a planar grid of 40 km * 1.5 km and imported into the Ranges software package (version 5; Kenward & Hodder 1996). To describe maximum range extent, the area of the minimum convex polygon around all fixes of each bird was calculated. To describe the area typically used by birds, the area of the fixed kernel enclosing 95% of the records was calculated (see above). Least-squares cross validation was used to select smoothing parameters to calculate the utilisation contours within home ranges.

To describe range structure, three cluster analyses were performed on each range, using the fixes from all records, records from intertidal habitats, and records from supratidal habitats. Nearest-neighbour joining priority was used to define distance of fixes from clusters, and all fixes were assigned to clusters. The cluster analysis yielded the number of separate cores within the range, distances between cores, and the partial area of the range. Partial area is the summed area of the cluster polygons divided by the area of a single polygon around all the clusters. It is an index of patchiness, where a value of 1 indicates a single range core, and values below 1 indicate a patchy range.

5.2.5 Measures of foraging on supratidal habitats

Birds were considered to be feeding supratidally where their location was above the most recent high water mark, and / or where their foraging substrate was beach-cast. Because the number of times a bird was observed feeding supratidally was related linearly to the total number of sightings ($r = 0.86$, $n = 140$, $p < 0.001$) and the number of days the bird had been colour-marked (defined as time elapsed from ringing until the last observed location; $r = 0.65$, $n = 140$, $p < 0.001$), indices of supratidal feeding were calculated. The first index was "supratidal feeding frequency", the number of times an individual was observed feeding supratidally as a proportion of the total number of sightings (feeding and roosting) of that bird. The second index was "supratidal feeding likelihood", the number of times an individual was observed feeding supratidally as a proportion of the number of times it had been seen in supratidal habitats. Supratidal feeding frequency gives a general index of how often a bird feeds supratidally, whereas supratidal feeding likelihood takes into account variation in the relative frequency of intertidal and supratidal sightings of each individual.

5.2.6 Measuring the association between fixes and beach-cast wrack

Spatial associations between individual fixes and the availability of beach-cast wrack were investigated by comparing the distances of birds to reliable sites for beach cast wrack with a random null model. A fix-site analysis was conducted using the Ranges computer software (version 5; Kenward & Hodder 1996) to look for an association between the fix locations of birds, and the locations of the sites that held beach-cast wrack (hereafter "sites") at least twice during winter 2000/2001 (see chapter 3). Envelopes with radii of half of the mean site-site nearest neighbour distance were constructed around the location of each beach-cast wrack site, and a sample of 1000 nearest-site distances for a set of random locations in the intertidal zone within the envelope was generated. The actual distance from each fix to the nearest site was then calculated and compared with the null model. Jacobs' Index (Jacobs 1974) was used to provide a single index describing the

degree of spatial association between beach-cast wrack sites and the locations of birds. This index was calculated as

$$J = (r - p) / [(r + p) - 2rp]$$

where r is the distance from the bird locations to the nearest site, and p is the distance from the randomised locations to the nearest site. The index gives a value of 0 if the observed and possible distances were the same, rising to +1 if the observed distances were small relative to possible distances (indicating attraction), and falling to -1 if the observed distances were large relative to possible distances (indicating avoidance; Kenward & Hodder 1996).

5.2.7 Data analysis

Most statistical analyses were implemented in SPSS version 11 (233 S. Wacker Drive, 11th floor, Chicago, Illinois 60606). Data were transformed where appropriate. Partial correlations were performed where it was necessary to test for an association between two variables while controlling for a third variable (Zar 1999).

All hypotheses were defined *a priori*, and data were not dredged for correlations. Where multiple correlations were performed on several variables used to describe features, in particular when comparing range size, and indices of supratidal feeding, there were dangers of spurious results emerging by chance. This was of particular concern for elucidating the relationship between supratidal feeding and range size. To minimise the chance of type I errors where multiple correlations were performed, results were considered biologically meaningful providing correlation coefficients were above 0.2 and p-values were well below 0.05.

5.3 Results

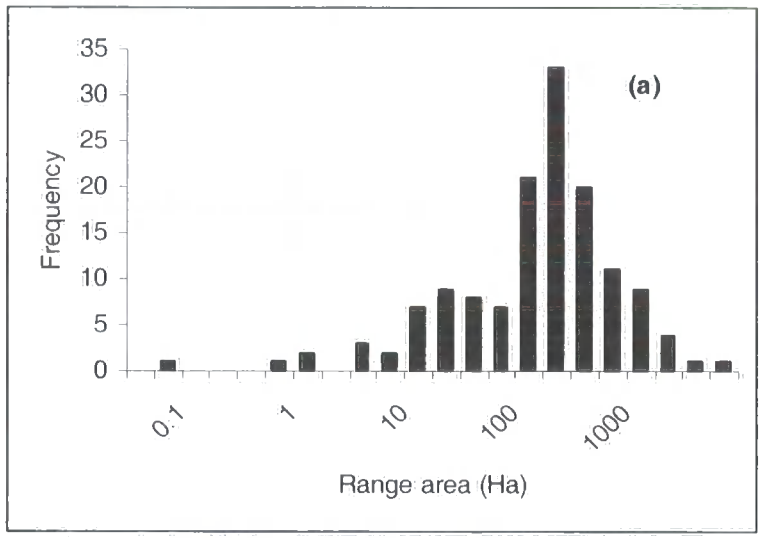
A total of 6780 observations of 227 colour-ringed birds was made, 4034 of the fixes being on intertidal substrates, 2595 on supratidal substrates, and 151 where substrate was unknown. After the dataset was trimmed, 4927 records of 140 birds remained, 2964 on intertidal substrates, 1854 on supratidal substrates, and 109 where substrate was unknown. Of the 4144 fixes where the activity of the bird was known, the bird was feeding in 3643 cases, and roosting in 501 cases. The relative frequency of intertidal and supratidal records was similar before and after trimming the dataset ($G_{adj} = 0.52$, d.f. = 1, $p = 0.471$).

5.3.1 Range size and structure

The mean home range size of all ruddy turnstones as expressed by the area of the 95% fixed kernel was 245.8 Ha, although there was much variation (n = 140, range: 0.04 - 3388 Ha, SD = 427.5)). Most birds had relatively small ranges, although some ranged much more widely, and distribution of range sizes was strongly positively skewed (figure 5.1 (a); skewness = 4.4, SD = 0.2). The mean range span was 6.0 km, although again there was large variation (n = 140, range: 0.1 - 30.6 km, SD = 7.2 km) and the distribution was positively skewed (figure 5.1 (b); skewness = 2.1, SE = 0.2), although markedly less so than the distribution of range sizes. Range size and range span were highly correlated ($r = 0.88$, $n = 140$, $p < 0.001$). The mean area of the minimum convex polygon enclosing all fixes for each bird was 491.7 hectares (range: 0.26 - 4357.4, SD: 811.7), suggesting that the minimum convex polygon was including large areas not used by the birds when estimating home range size. For this reason, the area of the 95% fixed kernel was used as the range size measure in all further analysis. There was no systematic change in range size along the length of the study area. The ranges showed a nested pattern, with smaller ranges falling completely within larger ranges.

Cluster analysis of the fixes revealed that many birds had multinuclear ranges and / or made excursive movements from the range core(s). Summary home range statistics for each bird are presented in Appendix 3. The ranges of 85 birds (61%) had only one core, while 55 ranges (39%) had more than one core (range 2-5 cores). Figure 5.2 shows representative mononuclear and multinuclear ranges. The mean partial area of the ranges was 0.7, indicating moderate to strong patchiness, although there was great variation in this statistic (range: 0.04 - 1, n = 140, SD: 0.38). Of the 55 birds with multiple range cores, the mean distance between cores was 4.1 km (range: 0.1 - 24.4, SD = 5.5).

Figure 5.1 (a) The distribution of range sizes of wintering ruddy turnstones as measured by the area of the 95% fixed kernel was highly positively skewed. The data are plotted on a log scale to show the detail of the distribution more clearly. Birds with larger range sizes tended to have multinuclear range structures, either as a result of abruptly switching to a new foraging site part-way through the study, or through making repeated excursive movements. (b) The distribution of range spans was also positively skewed, although this was less pronounced than in the distribution of range sizes. See text for details.



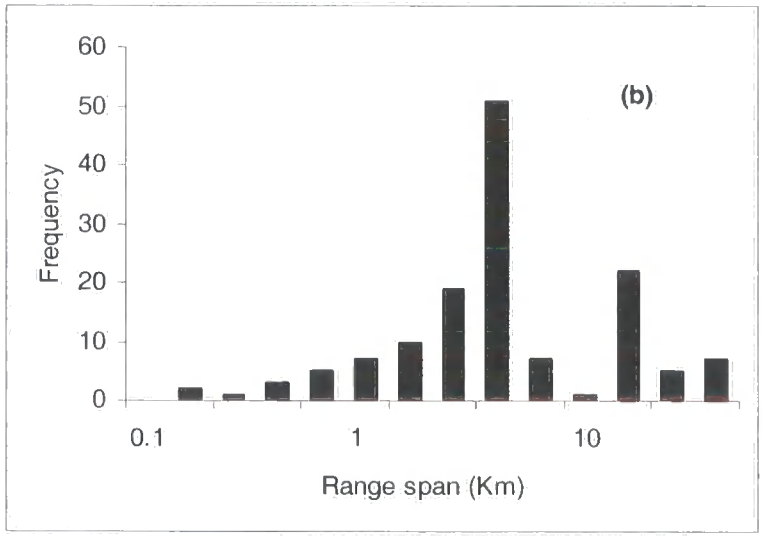
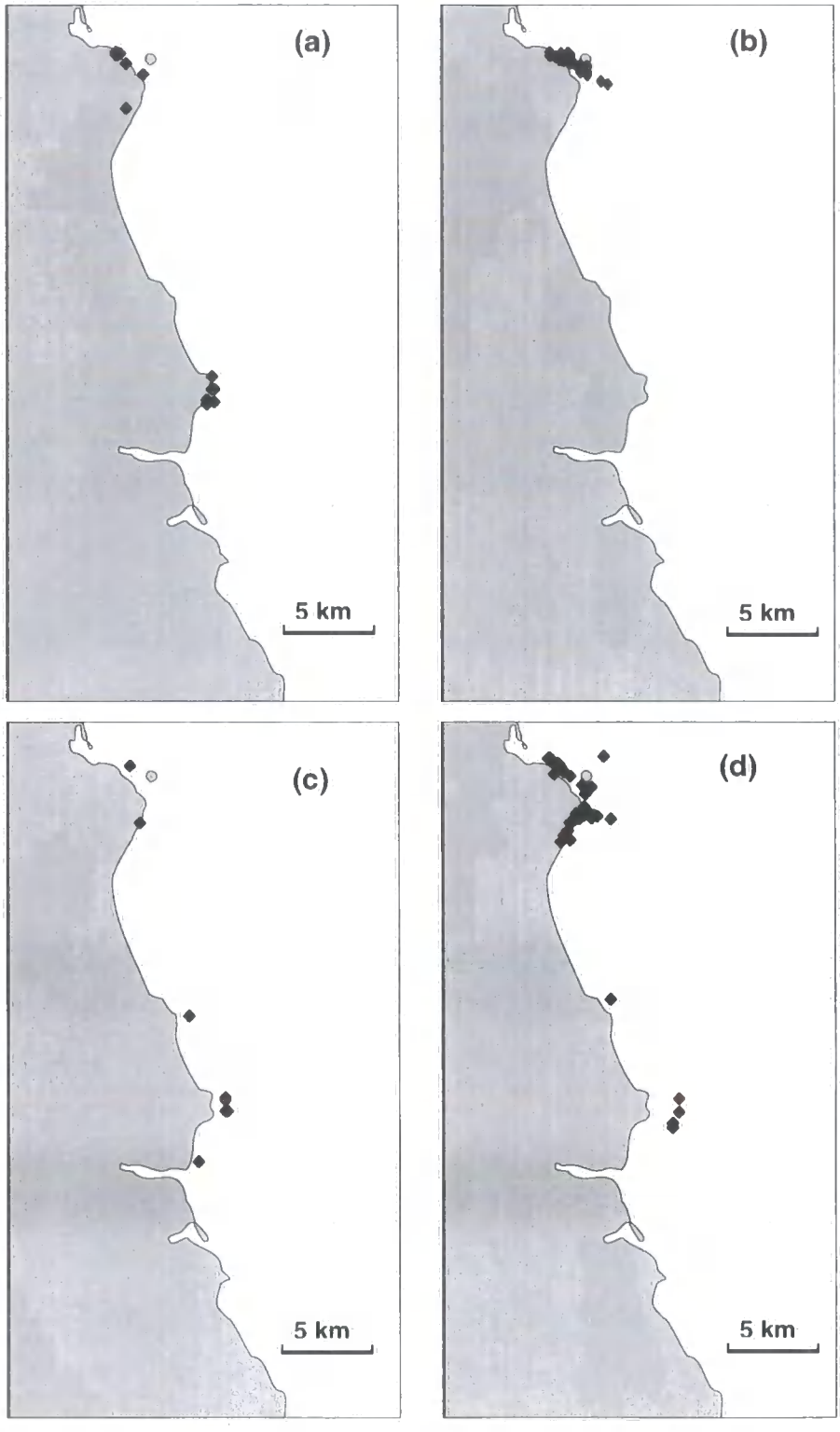
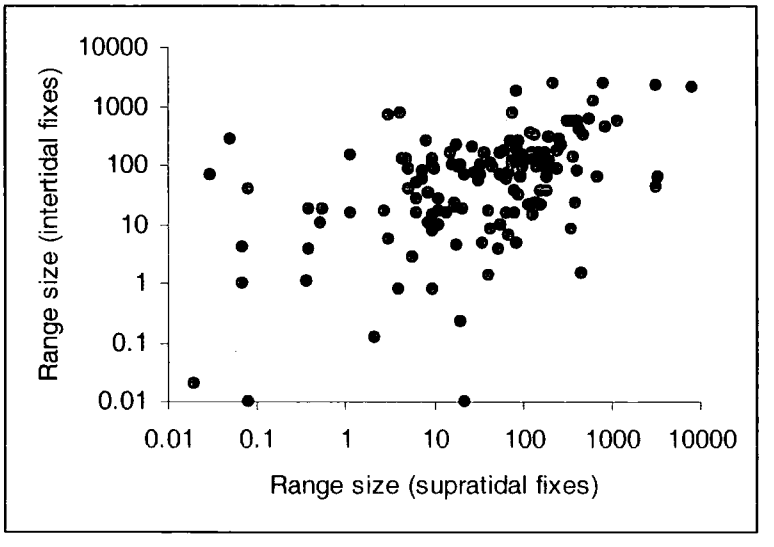


Figure 5.2 Representative range structures of ruddy turnstones in north-east England. (a) a widely-ranging bird with two discrete range cores (n = 21); (b) a narrowly-ranging bird with a single range core (n = 83); (c) an apparently itinerant bird with a large range (n = 18); (d) evidence of excursive trips from an otherwise stable range core (n = 109). Land is shaded grey.



Range sizes derived from intertidal fixes alone were not significantly different from range sizes derived from supratidal fixes alone (mean intertidal range size = 200 Ha, supratidal range size = 249 Ha; paired t-test: $t = 1.31$, d.f. = 139, $p = 0.194$). Furthermore, range size derived using only intertidal fixes was positively correlated with range size derived using only supratidal fixes (figure 5.3; $r = 0.52$, $n = 140$, $p < 0.001$), implying that intertidal and supratidal range sizes were being driven by the same factors. This relationship remained strong after controlling for sample size (partial correlation: $r = 0.46$, d.f. = 137, $p < 0.001$). In addition, the mean distance between consecutive fixes within a particular habitat type (i.e. ignoring intervening fixes in the other habitat) was very similar for supratidal and intertidal habitats (mean interfix distance for intertidal habitats = 1070 m, for supratidal habitats = 1146 m; paired t-test: $t = 0.25$, d.f. = 139, $p = 0.801$). These results suggest that birds were not making specific journeys (reflected in range size and structure) only to access a particular habitat type. Rather, foragers fed both intertidally and supratidally during excursive trips and following core switching.

Figure 5.3 Range size estimates broadly corresponded when using intertidal and supratidal fixes. Range size is the area in hectares of the 95% fixed kernel around the fixes. Note that the data are plotted on a log scale.

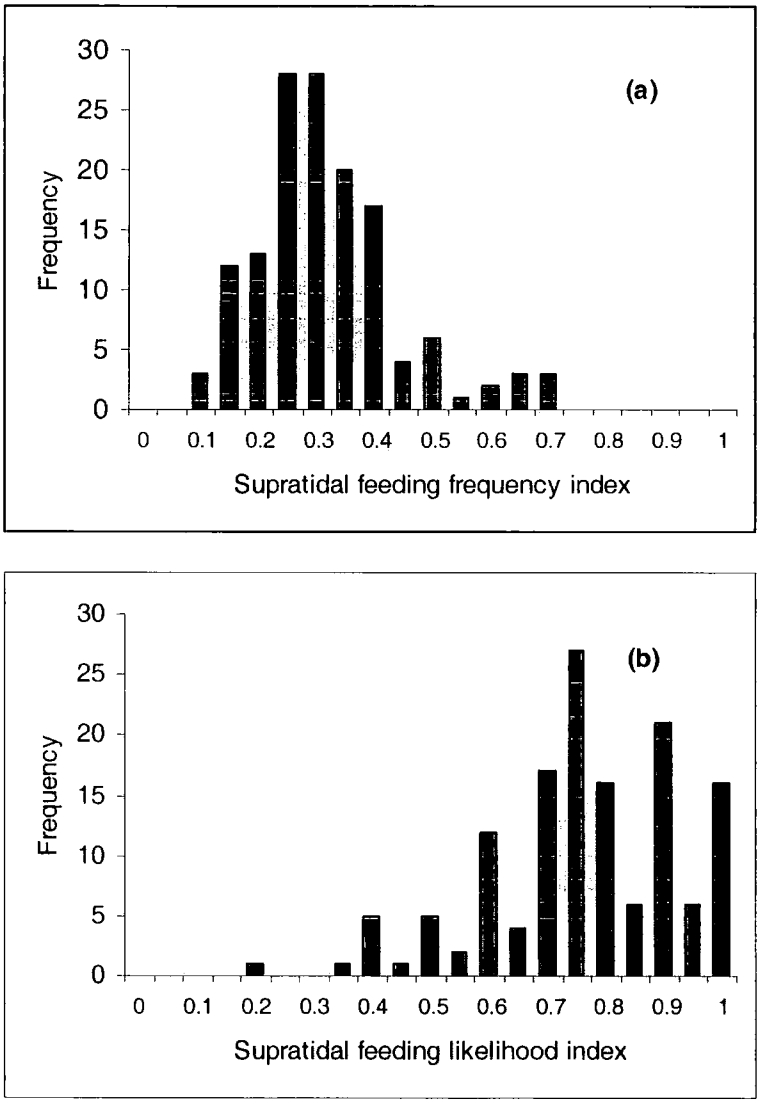


The scatter in figure 5.3 shows that there was much individual variation in relative range sizes on intertidal and supratidal habitats. Multiple regression analysis was used to investigate predictors of intertidal range size. A maximal model was constructed including supratidal range size, supratidal feeding frequency, and the number of intertidal fixes as predictors. All three terms retained significance in the final model ($F_{3,136} = 24.12$, $p < 0.001$). Not surprisingly, intertidal range size increased with both the supratidal range size and the number of intertidal fixes (supratidal range size: $t = 5.43$, $p < 0.001$; number of intertidal fixes: $t = 2.04$, $p = 0.044$). However, it was negatively related to supratidal feeding frequency ($t = -2.46$, $p = 0.015$). Birds with smaller intertidal range sizes, therefore, tended to feed more frequently on supratidal habitats, independent of the effects of sample size and supratidal range size.

5.3.2 Home ranges and supratidal feeding

The mean value of the supratidal feeding frequency index was 0.30 (figure 5.4 (a); range: 0.09 - 0.67, $n = 140$, $SD = 0.12$), indicating that on average, 30% of sightings of a given individual were of it feeding supratidally. The mean value for the supratidal feeding likelihood was 0.75 (figure 5.4 (b); range: 0.2 - 1.0; $n = 140$, $SD = 0.16$), indicating that on average, 75% of supratidal sightings of a given individual were of it feeding.

Figure 5.4 The frequency distributions of (a) supratidal feeding frequency and (b) supratidal feeding likelihood. Supratidal feeding frequency is the number of supratidal feeding sightings of a bird divided by the total number of sightings. Supratidal feeding likelihood is the proportion of sightings on supratidal habitats that were of a feeding bird.



Range size was negatively related to both indices of supratidal feeding using partial correlation controlling for the effect of the total number of fixes of each bird (supratidal feeding frequency: $r = -0.31$, $n = 140$, $p < 0.001$, supratidal feeding likelihood: $r = -0.29$, $n = 140$, $p < 0.001$). These results indicate that birds with smaller ranges were observed on supratidal habitats, and chose to feed rather than roost when on supratidal habitats, more frequently than birds with larger ranges. Although there was clearly a substantial amount of noise

in the relationships between the supratidal feeding indices and range size, and the partial correlation coefficients were rather low, there does appear to be a biological signal within these data. Both relationships were in the same direction, and were highly statistically significant. Taken together, these results indicate that birds with smaller ranges used supratidal habitats more frequently than birds with larger ranges.

5.3.3 Foraging movements

The typical length of foraging movements made by each bird was estimated by measuring the mean distance between the feeding fixes for that individual from the centre of its associated range core. This value was termed mean fix-core distance, and it was calculated for all habitats combined, and for intertidal and supratidal habitats separately. Mean fix-core distance for all habitats combined was negatively correlated with supratidal feeding frequency ($r = -0.31$, $n = 140$, $p < 0.001$), suggesting that birds that tended to make only short trips between foraging sites fed more frequently in supratidal habitats.

Multiple regression analyses were performed to investigate the relationships between the two supratidal feeding indices and fix-core distances. Models were constructed using total range size and the supratidal feeding indices as independent variables, and mean fix-core distance for intertidal and supratidal habitats separately as dependent variables. Not unexpectedly, total range size was positively related to mean intertidal fix-core distance in all analyses (all $p < 0.01$), indicating that birds with larger ranges tended to travel greater distances between both intertidal and supratidal foraging sites. Supratidal feeding frequency was negatively related to mean intertidal fix-core distance independent of the range size effect ($t = -2.27$, d.f. = 137, $p = 0.025$), but was not related to mean supratidal fix-core distance ($t = -1.5$, d.f. = 137, $p > 0.1$). These results suggest that birds that tended to use supratidal habitats more frequently travelled shorter distances to intertidal foraging locations, but still made longer journeys to supratidal foraging sites.

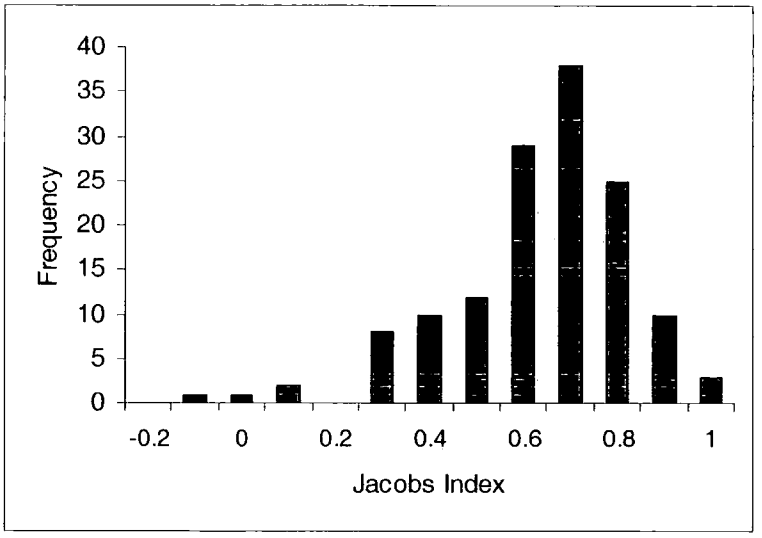
In other words, birds that were using a relatively small area of intertidal habitat tended to forage supratidally more frequently.

These results predict that supratidal foraging trips will be shorter in birds that keep shifting their range core, for example because they are responding to variation in food availability by shifting foraging site rather than over-compensating by high risk supratidal feeding. To investigate this, I again used the distance of each fix to the centre of its associated core. The mean distance of each fix to its core centre declined as the number of cores in the range increased (r_s = -0.30, n = 140, $p < 0.001$), suggesting that journeys to foraging and roosting sites were indeed shorter, on average, in birds that had multiple range cores.

5.3.4 The association between bird locations and beach-cast wrack sites

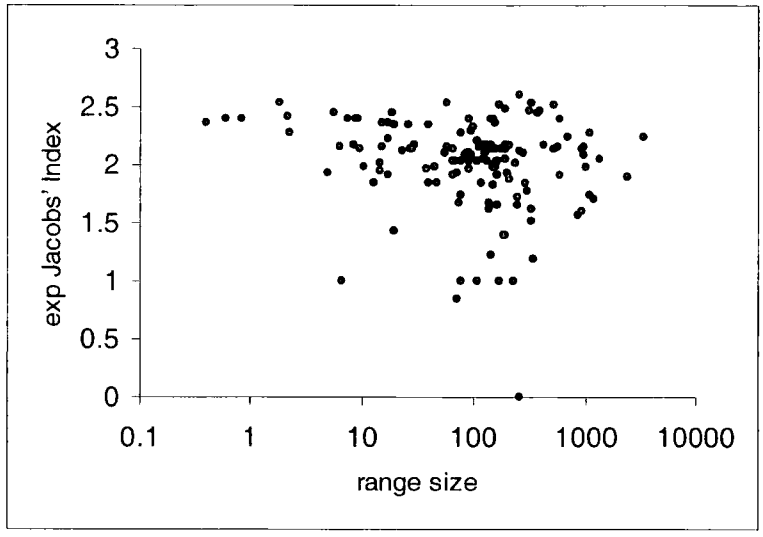
Twenty sites held beach-cast wrack more than once during winter 2000/2001 (see chapter 3). The fixes (feeding and roosting) of most birds were significantly closer to these sites than expected by random draw. The mean Jacobs' Index value comparing observed with expected distances between fixes and beach-cast wrack sites was 0.59 (figure 5.5; range: -0.14 - 0.93, n = 139, SD = 0.19), indicating generally a strong positive association between bird locations and sites where beach-cast wrack occurred relatively frequently. A one sample t-test confirmed that the Jacobs' Index values were significantly greater than the zero expected if birds were no more closely associated with beach-cast wrack sites than expected by chance (t = 36.56, d.f. = 137, $p < 0.001$). Figure 5.5 indicates that, although no birds strongly avoided beach-cast wrack sites, some were no more closely associated with them than expected by chance, with Jacobs' Index values close to zero.

Figure 5.5 Frequency distribution of Jacobs' Index values. Jacobs' Index indicates how closely birds are associated spatially with beach-cast wrack sites, and ranges from -1 (strong avoidance) to 1 (strong attraction).



The fix-site analysis was repeated using fixes from intertidal and supratidal habitats separately. The mean Jacobs' Index value was much higher when birds were on supratidal than intertidal habitats (mean on supratidal habitats = 0.68; intertidal habitats = 0.49; paired t-test: $t = 7.97$, d.f. = $p < 0.001$), indicating that birds were more closely associated with beach-cast wrack sites while foraging supratidally than intertidally. There was a negative correlation between range size and mean Jacobs' Index values incorporating fixes on all habitats ($r = -0.21$, $n = 139$, $p = 0.016$; figure 5.6), indicating that wide-ranging birds were not strongly attracted to beach-cast wrack sites. Supratidal feeding frequency was positively related to the Jacobs' Index values, after removing the effect of range size (partial correlation: $r = 0.28$, $n = 139$, $p < 0.001$). These results indicate that the birds most closely associated with beach-cast wrack sites tended to be narrow-ranging and those that fed more frequently on supratidal habitats.

Figure 5.6 The relationship between range size and Jacobs' Index, a measure of how closely birds were associated with sites that regularly held beach-cast wrack.



5.4 Discussion

5.4.1 Ranging behaviour and supratidal feeding

The fact that birds with smaller ranges tended to feed more frequently on supratidal habitats than birds with larger ranges indicated that birds were not making excursive trips to track the appearance of patches of profitable supratidal habitat. In fact, wide-ranging birds used supratidal habitats less frequently, and were less closely associated spatially with reliable sites for supratidal habitat patch formation. These results provide clear support for the avoidance hypothesis and allow the tracking hypothesis to be rejected.

Superficially, this result is counter-intuitive, as it might be expected that more widely-ranging birds will have more opportunities to access profitable supratidal resource patches. Rather, they appear to be more reluctant to use these habitats (and thereby pay costs such as elevated predation risk in return for high patch profitability) than more narrowly-ranging birds. There appears to be continuous individual variation in ranging behaviour and the propensity to feed supratidally. There are several possible explanations for these results.

Firstly, there are costs associated with making movements that must be considered when interpreting these results. Ruddy turnstones are highly site-faithful outside the breeding season (Metcalfe 1986), and they form stable dominance hierarchies that persist within and between winters (Whitfield 1985a). This implies that movement could result in social costs, as has been shown in stripe-backed wrens *Campylorhynchus nuchalis* Cabanis using patchy resources (Carolina Yáber & Rabenold 2002). For example, it might pay high ranking birds to remain site-faithful, so they can maintain their position socially. This exposes site-faithful birds to variation in intertidal food availability occurring at fairly coarse scales, from month-to-month and year-to-year rather than day-to-day. Resident birds would need to compensate for this variation by foraging supratidally when necessary. This means that high

ranking, resident birds pay the additional cost of elevated predation risk but have social stability. Lower ranking birds are not so tied to specific areas by the need to maintain their social position. This means they can respond to variation in intertidal habitat quality by spatial switching, thereby not needing to feed supratidally so frequently. This idea predicts that the propensity to forage on supratidal habitats will increase with rank (see chapter 6).

Although this is one possible explanation of results, others need to be considered. Because no experimental manipulations were made as part of this study, it is difficult to determine the direction of causality. For example, it is possible that status is determined by movement patterns rather than the other way around. Birds that choose to feed less frequently on supratidal habitats might need to range more widely to compensate for this, thereby lowering their social status through being itinerant. Removal experiments would be necessary to distinguish between these two possibilities.

It is possible that birds that have small ranges have a better knowledge of the arrival date of beach-cast material, so are better placed to predict when they will become profitable than more itinerant birds. This assumes that beach-cast wrack is a preferred foraging resource (after taking into account the costs of foraging there, such as elevated predation risk). If this is the case, we would expect foragers to use these resources, when available, throughout the tidal cycle, and that more birds would use supratidal habitats when there was more of it around. In fact, shorebirds mainly use supratidal habitats over the high water period (Fleischer 1983, Goss-Custard et al. 1996, Dann 1999, Masero & Perez-Hurtado 2001, Smart & Gill 2003), and the number of birds feeding supratidally is unrelated to the availability of supratidal habitats (chapter 6).

Another possible explanation is that those areas that tend to accumulate beach-cast wrack deposits (because of their topography) also offer profitable intertidal feeding, so high ranking birds tend to settle in these areas. Because these areas are higher quality, the birds would require only small intertidal home ranges and also make good use of the wrack deposits. Lower ranking

birds would be forced into more marginal intertidal habitats, that also more rarely have wrack deposits and are of poorer quality so require the birds to range more widely. It is currently unknown whether prey densities in intertidal and supratidal habitats covary spatially, and detailed invertebrate sampling would be required to answer this question. Again, this idea predicts that supratidal habitats are inherently preferred, so that they should be used more when more were available, and at all states of the tide. Also, the fact that smaller ranges were nested within larger ranges suggests that range size was determined more by individual identity than habitat quality.

As well as tending to have smaller ranges, birds that frequently fed on supratidal habitats were much more closely associated spatially with sites that regularly held beach-cast wrack. This suggests that the occurrence of beach-cast wrack is one of the factors governing site choice by ruddy turnstones. Indeed, Eaton (2001) found that a measure of beach-cast wrack appearance was a significant predictor of ruddy turnstone densities among sites. The results of this study suggest that beach-cast wrack is important in determining the foraging locations of site-faithful birds, but less important for itinerant birds. During excursive movements, birds fed intertidally and supratidally, and ranged over a similar area on both habitat types, further suggesting that excursive trips were not made to track supratidal foraging resources.

5.4.2 Range size and structure

The range size distribution of many organisms at many scales is approximately logarithmic (Gaston 1994), and previous study has shown a strong right skew in the home range sizes of ruddy turnstones (Metcalfe 1986). Most birds are narrow-ranging, and progressively fewer range more widely. There is no clear evidence of bimodality in the range size distribution (see figure 5.1), suggesting that ranging behaviour varies continuously between the two extremes. Range sizes in this study were much larger than those reported in Metcalfe (1986). This difference probably results from methodological differences between the two studies. The aim here was to

identify and include excursive trips and range core switching by examining ranging behaviour on a large scale and across many seasons, rather than investigate local associations among birds. This study has revealed great variation in range size and structure among individual ruddy turnstones, and shown that birds that ranged widely often occupied multiple range cores.

5.4.3 Conclusion

This chapter has shown that wide-ranging ruddy turnstones tended to feed less frequently on risky and unpredictable supratidal habitats than more narrow-ranging birds. Some birds made movements of varying distances, up to 30 km, and these movements sometimes resulted in birds switching their range core over time. Other birds remained more continuously site-faithful over time scales of several years, although there was evidence of a continuum of ranging patterns between these extremes. Highly site-faithful birds were closely associated with sites that regularly held beach-cast wrack, and may have compensated for the increased risk of predation on supratidal habitats with benefits gained from site fidelity such as a stable position within the dominance hierarchy or increased knowledge of when and where predator attacks may occur.

Chapter 6: Variation in foraging success affects the solution to the intake rate – predation risk trade-off

6.1 Introduction

A central theme in ecology has been understanding how animals respond to variation in food supply, in particular how interference (Fretwell & Lucas 1970; Meer & Ens 1997) and predation risk (Brown 1988) interact with food availability to influence foraging decisions. We know, for example, that individuals adjust their response to a given level of predation risk depending on their physiological status (Caraco 1979). Classical explanations for patch choice behaviour centre on the trade-off between maximising net energy intake while minimising predation risk (Sih 1980; Lima 1986; Houston et al. 1993, Lima 1998). In particular, the relationship between energy intake and predation risk is often portrayed as a fitness isopleth (Caraco 1979), with high-risk high-gain, and low-risk, low-gain strategists co-existing within the population at a frequency determined by the distribution of resources. This view has led to a tendency to interpret alternative foraging strategies involving ecological trade-offs as evolutionarily stable strategies (ESSs) resulting in equal fitness outcomes.

However, there are several other possible explanations for apparent alternative strategies of this kind. For example, it is easy to imagine a situation where a forager is forced into accepting an elevated predation risk in a novel patch as a result of low food availability in a previous patch. Rather than result in an ESS, this situation may lead to a fitness inequality between apparent "alternative" strategists. Where a forager's food intake rate falls below that required for energy balance, we may predict a spatial (McNamara & Houston 1986; Brown 1988) or temporal (Metcalfe et al. 1998) state-determined compensatory shift to a high risk but high profit foraging patch, where such exists. An ideal system for investigating these general phenomena is supratidal foraging by ruddy turnstones. Outside of the

breeding season, ruddy turnstones forage on rocky intertidal substrates when these are exposed by the tide (see chapter 1). Despite some circumstantial evidence of nocturnal foraging by ruddy turnstones (e.g. Clark et al. 1990, Robert et al. 1989, Schneider 1985), recent radiotracking data indicate that they rarely forage at night in the present study area (Eaton 2001).

Although many birds respond to high water by going to roost, even when this occurs during the period of daylight, some continue to feed on patchy and ephemeral supratidal deposits of beach-cast wrack (macroalgae of the genera *Fucus* and *Laminaria*), which are colonised by large numbers of coelopid wrack flies (Kirkman & Kendrick 1997; see chapter 3). These sites are usually in sheltered bays, close to cover from which raptors can launch surprise attacks, and there is good evidence that feeding supratidally exposes foraging shorebirds to elevated predation risk. For example, Whitfield (1985b) observed 33 attacks on wintering waders by sparrowhawks *Accipiter nisus* (L.), one of the main predators of ruddy turnstones. Thirty of these attacks, including all seven successful ones, were made on birds feeding on the strandline rather than lower down the shore. Moreover, shorebirds that roost over the high water period generally choose exposed sites, and it has been shown that redshanks use foraging sites further from cover on days of high raptor activity (Hilton et al. 1999a). Why then do we see some foragers choosing high-risk high-gain patches over the high water period, while others stop feeding altogether? This question is particularly pertinent given the patchy, ephemeral and unpredictable nature of supratidal foraging resources (see chapters 2 & 3). At least four hypotheses could account for these apparent alternative strategies (table 6.1 on page 113 summarises the predictions made by each of the hypotheses).

6.1.1 Hypothesis (a): Resource sharing (e.g. ESS)

The most parsimonious explanation is the existence of two strategies with equal payoffs (supratidal feeding and non supratidal feeding) within the population. This equates to the classical view of ecological trade-offs. Supratidal feeders trade off the increased predation risk associated with supratidal feeding with increased intake rates gained from such foraging, while non supratidal feeders opt for reduced predation risk at the expense of lower intake rates. The decision to feed supratidally over a given high water period depends on the availability of high profit patches, so the resource sharing hypothesis predicts a positive relationship between beach-cast wrack availability and the proportion of the population feeding over high water. It also predicts lower intake rates per unit time and/or time spent feeding for supratidal feeding strategists while foraging on intertidal rather than supratidal substrate, because these individuals can afford to spend more time engaged in vigilance and maintenance behaviours.

6.1.2 Hypothesis (b): Interference competition

Individuals may forage supratidally because these areas contain the most profitable food resources. Interference on supratidal resource patches excludes lower ranking individuals, limiting a proportion of the population to intertidal feeding alone (a truncated phenotype distribution; Parker & Sutherland 1986). By feeding on high-risk high-gain patches particularly over high water, a forager reduces the total amount of time it needs to spend foraging over the whole tidal cycle, and any elevated predation risk while feeding supratidally is offset by the high quality of supratidal habitat patches (particularly beach-cast wrack deposits) and the release of time for vigilance and maintenance behaviours while foraging intertidally.

The interference competition hypothesis predicts close tracking of the availability of supratidal food resources, as the profitability of these drives the

decision to feed over any given high water period. It also predicts that supratidal feeding strategists will spend less time foraging and/or show lower intake rates when foraging intertidally than non supratidal feeding strategists because of the time saving gained over the high water period. A third prediction is that beach-cast wrack deposits will be used independently of tidal state, because supratidal resources are inherently preferred.

6.1.3 Hypothesis (c): Reluctant compensation with (i) extrinsic or (ii) intrinsic variation in intake rate

High risk feeding may be undertaken facultatively when energy intake rate falls below that required to balance an individual's energy budget. Energy intake could vary as a result of chance, extrinsic factors such as weather conditions or variation in intertidal habitat quality ((i) above), or fixed intrinsic factors such as individual foraging efficiency, competitive ability, or predator avoidance capability ((ii) above). The consequences of variation in food availability through extrinsic factors will depend greatly on individual characteristcs such as foraging efficiency and the ability to respond to variation in intertidal food availability by switching to different intertidal areas. We might expect individuals with low foraging efficiency to be disproportionately affected by reduced food availability since their energy intake rate at the low-risk low-gain patch may frequently fall below the minimum necessary for body maintenance. This may not be the case where animals can make spatial switches to higher quality intertidal areas, although there may be other costs associated with such itinerancy. Individuals forced to feed supratidally over a particular high water period to compensate for reduced low water intake pay the cost of an absolute elevation in daily predation risk, although the effect on mortality risk may be less pronounced if some animals can switch between different intertidal habitat patches. Chapter 5 described the association between supratidal feeding and alternative spatial strategies, and this chapter aims to identify the correct general explanation for supratidal feeding in ruddy turnstones.

The reluctant compensation hypotheses predict that the number of birds feeding supratidally will be independent of the availability of supratidal food resources, as the system is driven by variation in food intake while foraging intertidally. They also predict that individuals feeding supratidally will spend more of their time on intertidal habitats foraging than non supratidal feeding individuals, as the high water feeding is necessary to top up an inadequate energy intake during low water. Reluctant compensation with primarily intrinsic variation in intake rate predicts that supratidal feeders will show permanently lower foraging efficiency than non-high water feeders. This implies that supratidal feeders should in general be lower ranking than non supratidal foragers. Reluctant compensation with primarily extrinsic variation in intake rate predicts only temporarily lower foraging efficiency than non high water feeders, and makes no direct prediction about the relative ranks of supratidal and non supratidal foragers.

Table 6.1 Predictions made by each of the four hypotheses for supratidal feeding.

	Prediction			
Hypothesis	Relationship between supratidal food availability and number of birds feeding supratidally	Foraging efficiency of persistent supratidal feeders versus intermittent supratidal feeders	Relative proportion of time on intertidal habitats spent feeding by persistent supratidal feeders	State(s) of tide when supratidal habitats used
(a) Resource sharing (e.g. ESS)	positive	equal	low	whole cycle
(b) Interference competition	positive	high	low	whole cycle
(c) i. Reluctant compensation with extrinsic variation in intake rate	none	temporarily low	high	high water only
(c) ii. Reluctant compensation with intrinsic variation in intake rate	none	permanently low	high	high water only

6.2 Methods

6.2.1 Supratidal foraging by ruddy turnstones

This work was conducted on the 39.5 km stretch of rocky coastline between St. Mary's Island (55º 4' 37N 1º 27' 8W) and Amble (55º 19' 60N 1º 34' 60W), on the north-east coast of England (see chapter 1 for a description of the

study area). Data were collected during winter 2000/2001 unless otherwise stated. Winter is here defined as the months of November to February inclusive, a period when migratory activity of ruddy turnstones is minimal and populations are stable (Eaton 2001). Numbers of ruddy turnstones feeding over high water were recorded weekly throughout the winter. During each count, the entire 39.5 km stretch of coastline was checked for feeding birds. High water was defined as the period two hours either side of high tide itself. The location, substrate and number of birds comprising each high water feeding event were recorded, as was the distance from the foraging flock to the extreme high water mark. In addition, roosting ruddy turnstones were counted, when seen. Two roost sites were located on offshore islands not visible from the mainland, so these sites could not be counted during the weekly sessions, although complete counts were made at appropriate stages of the tide every two weeks as part of another study. Where there was a clear disparity between the high water counts and the total present in the study site as estimated from the complete counts, the complete count nearest in time to the high water survey was used to derive a value for the number of birds roosting out of sight.

Because the number of times a bird was observed feeding supratidally was related linearly to the total number of sightings ($r = 0.86$, $n = 140$, $p < 0.001$) and the number of days the bird had been colour-marked ($r = 0.65$, $n = 140$, $p < 0.001$), indices of supratidal feeding were calculated. The first index was "supratidal feeding frequency", the number of times an individual was observed feeding supratidally as a proportion of the total number of sightings of that bird. The second index was "supratidal feeding likelihood", the number of times an individual was observed feeding supratidally divided by the number of times it had been seen roosting supratidally. Supratidal feeding frequency gives a general index of how often a bird feeds supratidally, whereas supratidal feeding likelihood takes into account variation in the relative frequency of intertidal and supratidal sightings of each individual.

6.2.2 Availability and quality of beach-cast wrack

The availability and quality of beach-cast wrack deposits along the study site were also measured on the same day as the high water counts. See chapter 3 for details of obtaining beach-cast wrack measurements. Measures of the availability and quality of supratidal foraging resources were derived for each week's data; these were an index of beach-cast wrack deposit spread, total combined length of all deposits, and total combined volume of all deposits. To describe overall patchiness of supratidal resource availability, beach-cast wrack deposit spread was expressed as the number of 500 m divisions of the study site containing deposits each week. Total length of wrack deposit could potentially have been used by foragers to assess habitat availability, but as there was no relationship between weekly combined length of wrack deposits across the study site and mean temperature ($r = -0.17$, $n = 15$, $p = 0.543$, maximum temperature ($r = 0.03$, $n = 15$, $p = 0.993$), or the predicted total number of available coelopid wrack flies ($r = 0.01$, $n = 15$, $p > 0.996$), total length was unlikely to indicate patch quality to foragers. Mean deposit age, mean and maximum coelopid density, and total coelopid availability in the deposits were therefore used as indicators of aspects of patch quality, although it is likely that only deposit age could be used directly by the birds in making *a priori* foraging decisions.

6.2.3 Time spent foraging by intertidal foragers

During the low water period (within two hours either side of time of low tide), colour-ringed ruddy turnstones were selected at random and the time spent foraging within a five-minute period was recorded. A bird was considered foraging if it was head-down and actively searching for or handling food. To reduce effects of habitat selection, data were collected only on birds foraging on rocky intertidal areas dominated by *Fucus* spp. The number of times each colour-ringed bird was observed feeding in the high water period was obtained from the database of sightings of colour-ringed birds made during

the course of five years' work on the present study population (see chapter 5 for details of how those data were collected). Similarly, estimated distances to the extreme high water mark from the centre of each of 143 flocks observed foraging intertidally were extracted from the sightings database.

6.2.4 Individual rank, sex and biometric data

Observations of aggressive encounters involving colour-marked birds were collected between October 1996 and November 2002[1]. The outcome of each aggressive encounter was recorded. Too few dyadic interactions between colour-marked birds were made to allow construction of a robust dominance matrix, so the proportion of victories by each bird was used as a surrogate measure of rank. To stabilise these proportions, only individuals with more than five recorded aggressive encounters were included in any analysis.

Information on the sex of 54 colour-marked birds was supplied by M. Eaton (see Eaton 2001 for details). Birds were sexed for that earlier study using a combination of DNA sex-determination and field-based observations of birds in Spring as they acquired breeding plumage. The two methods showed a very high level of concordance, so birds sexed by either technique were included in the current analysis.

Wing length, mass and age of birds trapped for colour-marking were recorded. Seventeen birds known to be juveniles (i.e. known to be hatched in the most recent breeding season) were ringed during the course of the work. The dates of subsequent sightings of these birds were used to calculate their age in months at each sighting, assuming the bird hatched in the July prior to ringing. In arctic Canada, ruddy turnstones usually hatch in mid-July, and there is very little inter-annual variability (Nettleship 1973). Records of known-age birds were extracted from the database of sightings of colour-

[1] Observations were made by M. Eaton until 28 March 1999 and by R. Fuller after 4 October 1999

marked birds. For each sighting, the bird's behaviour was recorded as feeding or roosting, and the habitat as supratidal or intertidal.

6.2.5 Data analysis

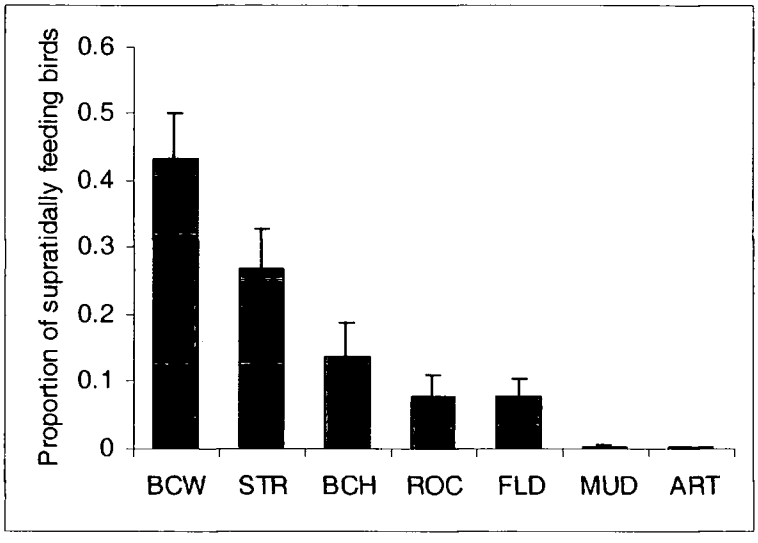
Preliminary exploration of beach-cast wrack and bird count data indicated that no important autocorrelation or partial autocorrelation existed within the time series of 16 weeks (correlation coefficients were within the 95% confidence limits at all lags), and as such, each week's data could be treated as independent samples. Biologically speaking, the birds' decisions to feed over the high water period during each weekly count were likely to be independent of their decisions during the previous survey (14 tides earlier). The association between high water feeding and various measures of beach-cast wrack availability was therefore tested using uncorrected parametric correlation.

6.3 Results

6.3.1 Supratidal habitat choice

Total numbers of ruddy turnstones in the study were stable throughout the study period (mean = 437, range: 414 - 461). A mean of 54.4% of the population fed supratidally over any given high water period, though this varied from 33.8% to 72.0%. There were no significant monthly changes in the relative numbers of birds feeding over high water (G_{adj}: = 6.12, d. f. = 3, $p > 0.1$). Birds were observed foraging on seven supratidal substrate types, with the numbers feeding on beach-cast wrack and to a lesser extent strandline debris being significantly greater than expected from an even distribution (figure 6.1; Friedman test: $\chi_r^2{}_{4,16} = 52.2$, $p < 0.001$). Beach-cast wrack deposits covered a very small fraction of the area of the study site (mean 403 m or 0.8% of the total coastline, range 90 - 810 m), indicating strong selection of this substrate.

Figure 6.1 Choice of supratidal foraging substrates by ruddy turnstones feeding over the high water period. The proportion of high water feeding birds is the mean of the 16 weekly proportions for each substrate. Based on 452 high water feeding events during winter 2000/01. Error bars are +1 SE. BCW – beach-cast wrack, STR – strandline debris, BCH – beach, ROC – rocks, FLD – fields, MUD – mudflat, ART – artificial structures. Post hoc tests showed that beach-cast wrack and strandline debris were preferred over the other substrates (Wilcoxon tests: beach-cast wrack all $p < 0.02$; strandline debris all $p < 0.05$).



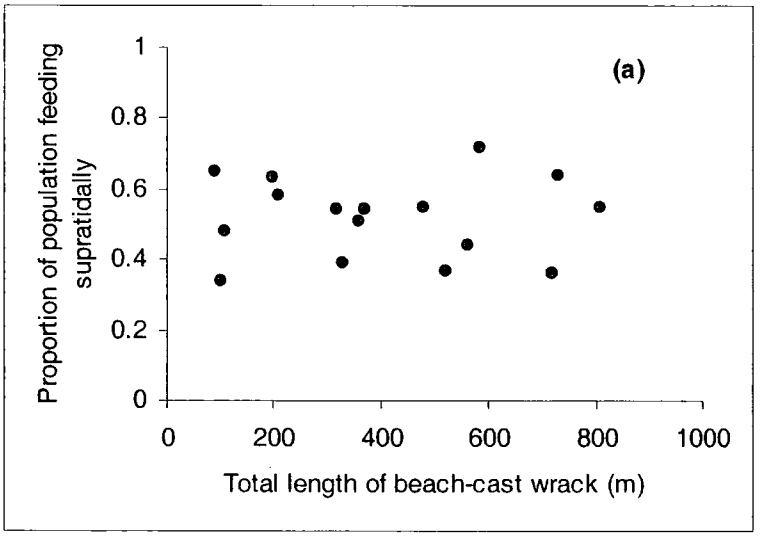
Flocks feeding supratidally over the high water period were much closer to the extreme high water mark than flocks feeding intertidally (mean distance on supratidal habitats = 6.7 m, SD = 3.0; on intertidal habitats = 175.2 m, SD = 90.9; unpaired t test: $t = 22.16$, d.f. = 59, $p < 0.001$).

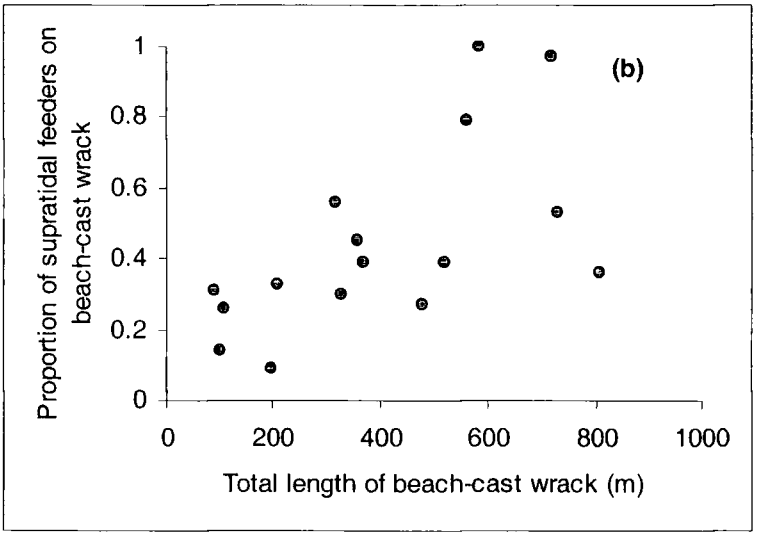
6.3.2 Supratidal feeding and resource availability

The proportion of the ruddy turnstone population feeding supratidally was independent of beach-cast wrack availability as measured by length of deposits (figure 6.2 (a); $r = 0.08$, $n = 16$ weekly surveys, $p > 0.7$) and volume ($r = -0.11$, $n = 16$, $p > 0.6$). Furthermore, there was no significant relationship between the two measures of patch quality and the proportion of birds feeding supratidally (estimated total coelopids present in the study area: $r = 0.13$, $n = 15$, $p = 0.641$, mean coelopids per wrack deposit: $r = 0.21$, $n =$

15, p = 0.446). However, the number of birds feeding on beach-cast wrack deposits expressed as a proportion of the total number feeding supratidally was strongly correlated with beach-cast wrack availability as measured by spread (r = 0.67, n = 16, p = 0.008) and length of deposits (figure 6.2 (b); r = 0.59, n = 16, p = 0.012), but not by volume (r = 0.35, n = 16, p = 0.164) or quality (total coelopids: r = 0.13, n = 15, p = 0.625, mean coelopids per wrack deposit: r = -0.03, n = 15, p = 0.990). These results suggest that the decision to feed supratidally was not driven by beach-cast wrack availability or quality, although birds feeding supratidally preferred beach-cast wrack deposits when their availability was higher.

Figure 6.2 (a) The proportion of the ruddy turnstone population feeding supratidally each week was independent of availability of beach-cast wrack deposits as measured by their combined length. (b) The proportion of supratidally feeding birds that were using beach-cast wrack deposits increased with their availability as measured by combined length.

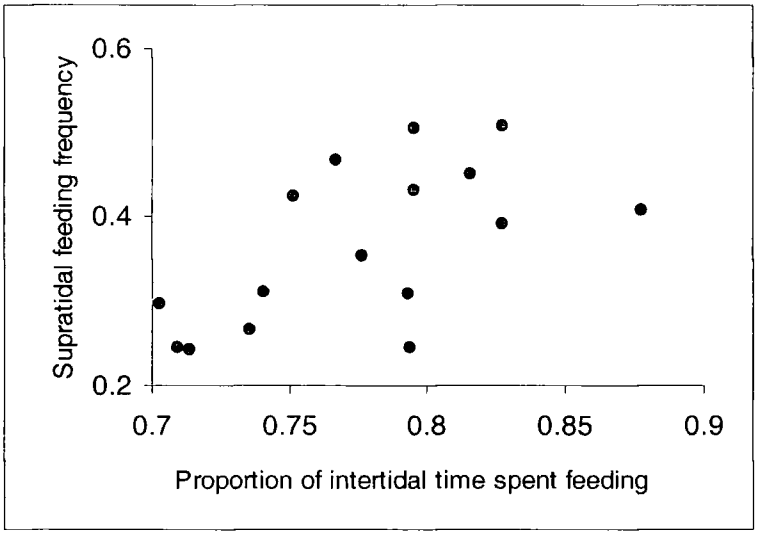




6.3.3 Supratidal feeding and individual characteristics

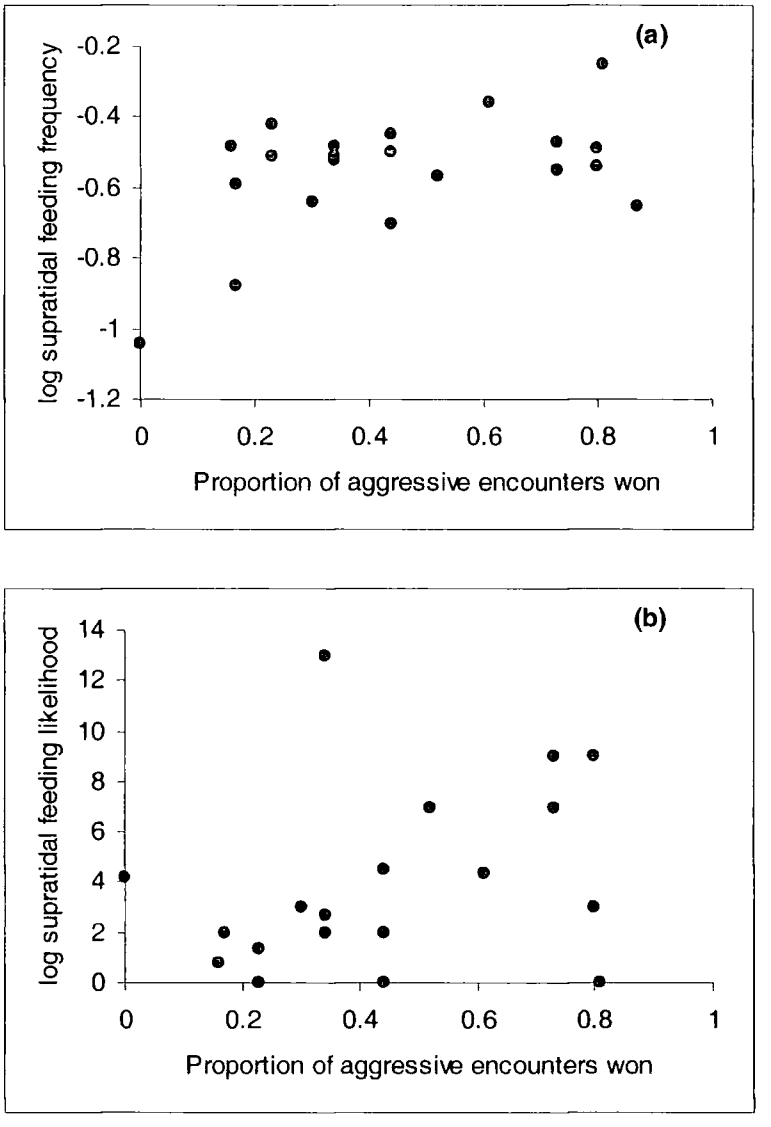
Intertidal foraging data were collected for 16 birds marked with unique colour-ring combinations. Supratidal feeding frequency was significantly positively correlated with the proportion of time a bird spent foraging in a five minute period during low water (figure 6.3; $r_s = 0.60$, $n = 16$, $p = 0.014$). Thus, birds that tended to feed supratidally spent a higher proportion of their time foraging when on intertidal habitats.

Figure 6.3 The proportion of its time on intertidal habitats an individual spent foraging during a five-minute period increased with the proportion of times it was observed feeding supratidally. Supratidal feeding frequency is the proportion of total sightings of each bird that were of it foraging on supratidal habitats.



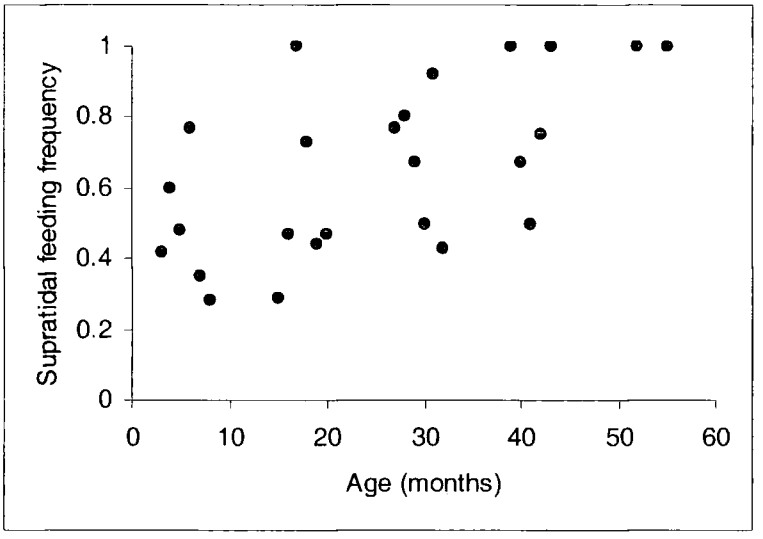
High water feeding frequency and high water feeding likelihood were both positively correlated with the proportion of victories by individuals (figure 6.4; supratidal feeding frequency: $r = 0.47$, $n = 27$, $p = 0.013$, supratidal feeding likelihood: $r = 0.44$, $n = 23$, $p = 0.036$). The proportion of victories by birds involved in aggressive encounters did not differ between the sexes ($U_{4,5} = 8.5$, $p = 0.730$). The sample size was low on this analysis because there were few sexed birds with more than five aggressive encounters recorded. I therefore conducted a further comparison using all birds where more than one aggressive encounter had been recorded (9 females and 19 males). There remained no significant difference between the sexes in proportion of victories ($U_{9,19} = 72.5$, $p = 0.530$). Males fed supratidally more frequently than females ($U_{16,38} = 195.5$, $p = 0.040$; males = 0.31, females = 0.25), although supratidal feeding likelihood did not differ between the sexes ($U_{16,38} = 278.15$, $p = 0.629$).

Figure 6.4 Birds that won more aggressive encounters tended to feed more frequently on supratidal habitats (a) and sightings of these birds at high water were more likely to be of them feeding than roosting (b). Proportion of aggressive encounters won arcsine transformed prior to analysis. See text for details of supratidal feeding indices.



Four hundred and forty-eight sightings were made of known-age birds. Ages ranged from three to 55 months. Supratidal feeding frequency was positively correlated with age (figure 6.5; $r = 0.60$, $n = 26$, $p < 0.001$), although there was no significant relationship between supratidal feeding likelihood and age ($r = -0.36$, $n = 26$, $p = 0.284$).

Figure 6.5 Supratidal feeding frequency increased with age. Supratidal feeding frequency is the number of supratidal sightings of a bird divided by the total number of sightings.



Wing length and mass at ringing were known for 120 birds. The two variables were entered into a principal components analysis to extract a single measure of size. The first component of the solution (PC1) explained 63% of the variation in the data. There was no relationship between bird size (PC1) and either of the indices of supratidal feeding (supratidal feeding frequency: $r = 0.02$, $n = 120$, $p = 0.986$, supratidal feeding likelihood: $r = 0.07$, $n = 95$, $p = 0.516$).

Flock size (the mean size of flocks in which a given bird was found) on supratidal habitats decreased as supratidal feeding frequency increased ($r = -0.38$, $n = 139$, $p < 0.001$), although supratidal feeding likelihood did not change with flock size ($r = -0.15$, $n = 107$, $p = 0.134$). The size of intertidal flocks was unrelated to either supratidal feeding measure.

6.4 Discussion

That birds foraging intertidally were much further away from the extreme high water mark than birds foraging supratidally over high water suggests strongly that feeding supratidally incurred elevated predation risk. Hunting sparrowhawks can attain a maximum flight speed of 25 m per second for short bursts (Newton 1986, Hilton et al. 1999b). As this is substantially slower than escape flight speeds of shorebirds, sparrowhawks must rely on surprise to mount a successful attack (Newton 1986, Cresswell 1996). The difference in distance to cover means that ruddy turnstones foraging intertidally would have an average of 7 s (175.2 / 25) to detect a sparrowhawk after it had left cover, whereas those foraging supratidally would have only 0.27 s (6.7 / 13.89). Given that response differentials of 0.7 s have been shown to influence the mortality risk of foraging redshanks *Tringa totanus* from a particular predator attack (Hilton et al. 1999b), this additional warning time is likely to result in a substantial difference in predation risk.

6.4.1 Which hypothesis?

These data clearly support one of the reluctant compensation hypotheses. The proportion of ruddy turnstones feeding supratidally was independent of beach-cast wrack availability, indicating that birds were not using supratidal resource availability as a cue for supratidal feeding. This rules out ESS-type and interference competition explanations (table 1). Moreover, persistent supratidal feeders spent more of their time in intertidal habitats feeding than intermittent supratidal feeders, suggesting that they had reduced energy intake while foraging intertidally, something predicted by both reluctant compensation hypotheses (table 1). Low foraging efficiency is not necessarily a permanent feature of supratidal feeders, but low energy intake on a particular low water period will lead to supratidal feeding. As there was great individual variation in the tendency to feed supratidally (see chapter 4) purely extrinsic control, for example by weather conditions seems unlikely. It is

possible, however, that extrinsic factors may interact with intrinsic factors to influence energy intake while foraging intertidally.

These results indicate that the decision to feed supratidally is driven by variation in energy intake during the low water period. The reasons for this variation in energy intake are unclear. Supratidal feeders behave as the reluctant compensation models predict, apparently topping-up over high water as a result of inadequate low water energy intake and thereby being forced into paying the cost of increased predation risk. However, these birds tend to be older and higher ranking than non-supratidal feeders, and it appears that they are feeding supratidally to avoid switching intertidal foraging area (see section 5.4.1 on page 104). Although older birds are more experienced foragers, they may also have more to lose from itinerancy.

It has been shown that high ranking ruddy turnstones tend to have smaller home ranges than lower ranking birds (Metcalfe 1986). This may be because they can defend a stable resource base. This study has shown that high ranking birds, particularly males, are also more likely to feed on risky but profitable supratidal habitats. It is possible that higher ranking birds have a greater energy demand than lower ranking birds. It is known that BMR increases with rank (Hogstad 1987), although it is unclear to what extent this affects daily energy expenditure (Bryant & Newton 1994). High ranking birds also tend to be involved in more aggressive interactions than lower ranking birds (Järvi et al. 1987), who may avoid confrontation with dominants (Metcalfe 1986).

There is some support for the idea of reluctant compensation from studies of supratidal feeding in oystercatchers (Goss-Custard et al. 1996; Caldow et al. 1999; Stillman et al. 2000b). It has been shown that individuals of low foraging efficiency are more likely to use supratidal supplementary food supplies than individuals of higher foraging efficiency, although in the oystercatcher system, supplementary feeding areas are less profitable than

intertidal substrates. The current work suggests that, where the supratidal foraging substrate is of sufficient quality, and intertidal habitats are relatively stable, it may in fact pay higher ranking birds to adopt a foraging strategy involving use of substrates where predation risk is high (see chapter 7). I have excluded the possibility that variation in high water food resource availability drives the decision to feed over high water, and considered explicitly the effects of predation risk and considerations arising from the maintenance by individuals of their position in the dominance hierarchy.

6.4.2 Modelling the decision to feed supratidally

The ruddy turnstone example provides a template for a more general model describing how individuals should choose between low-quality low-risk patches and high-quality high-risk patches.

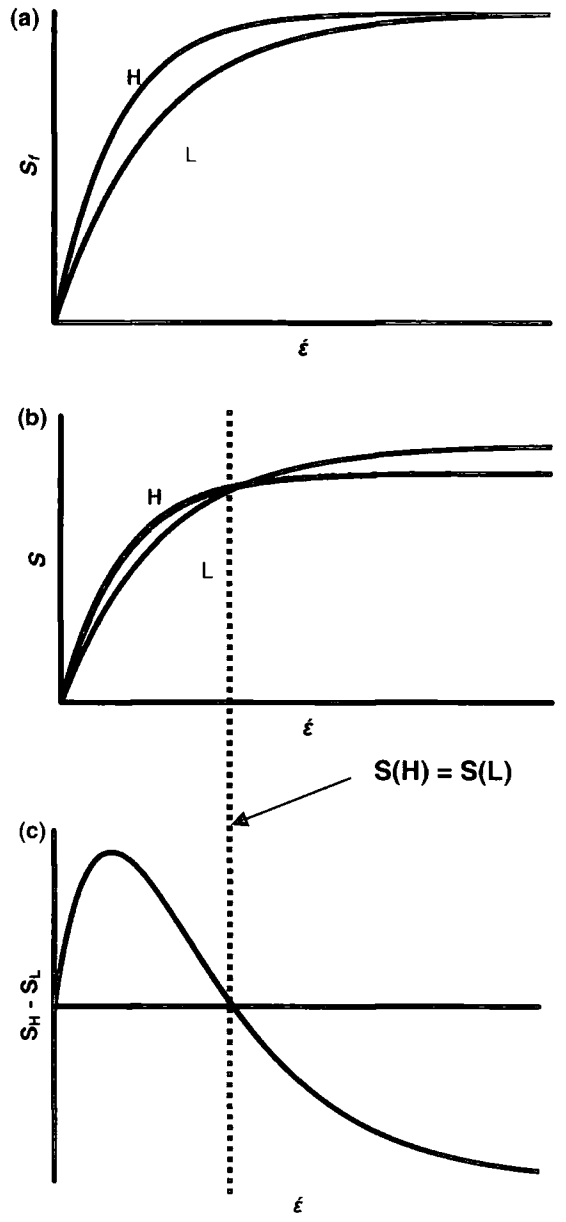
If high profit substrates incur elevated predation risk, foragers may only choose to pay this increased cost when energy intake in low profit substrates has proved inadequate. In the ruddy turnstone system, inadequate energy intake can result from the forager being unwilling to make excursive movements to track intertidal resource availability. This is important because it implies that individuals will vary in the way they manage the trade-off between energy intake and predation risk, and while such foraging may be adaptive (*sensu* Sih 1980), fitness outcomes of the "alternative strategists" may be different, suggesting a threshold for switching intertidal foraging site if energy intake on the low-quality low-risk remains low. This system can be described with a very simple model (figure 6.6). Although this model is described in terms of "strategies", in reality there will be a continuum of intermediate states between the two extremes. The alternative strategies are *L* to feed only on the low quality low risk substrate (i.e. feeding during the low water period on rocky shores), and *H* additionally topping-up energy intake by continuing to feed over high water on high quality high risk substrate. Here, we measure fitness by overall survivorship *S* (the product of the

probability of avoiding starvation S_f and the probability of avoiding predation S_p), as we are dealing with a non-breeding population (Caraco 1979; Lima 1986).

Relationships between foraging efficiency ε and S_f for the two strategies ($S_f(L)$ and $S_f(H)$) will take the form of convex curves through the origin (figure 6.6 (a)). Where ε=0, an individual will certainly die, but the rate of increase of S_f will diminish with increasing ε. As the density of available food in high water feeding substrates d_H is far greater than in low water substrates d_L, $S_f(H)$ will never be lower than $S_f(L)$, although the curves will meet at the origin and asymptote at the same level. Therefore, purely considering S_f, an individual should always choose a high water foraging strategy (figure 6.6 (a)), although there is little difference between the two strategies for individuals that achieve very high or very low energy intake while foraging intertidally. Such relationships can be described explicitly in a number of different forms, for instance $S_f(L)=1-\exp(-d_L*\varepsilon)$ and $S_f(H)=1-\exp(-d_H*\varepsilon)$.

Estimates for predation-based survivorship S_p on the two foraging substrates take the form of constants p_L and p_H for low and low+high water foraging substrate predation-based survivorship respectively ($S_p(L)$ and $S_p(H)$). Because $p_H<p_L$, different strategies for maximising S now emerge depending on the intertidal energy intake achieved by the forager (figure 6.6(b)). The immediate fitness implications of the two strategies will depend on the product of S_f and S_p for each value of ε (figure 6.6 (c)). Within a general trend of increasing survivorship with intertidal energy intake, individuals doing poorly at low water will maximise survivorship by following the supratidal feeding strategy, whereas individuals doing well while foraging intertidally at low water should avoid high risk feeding substrates even though they are of high food quality. The relative importance of choosing the correct strategy therefore also varies with ε (figure 6.6(c)). At an intermediate level of ε, the strategies will have equal fitness consequences (i.e. $S_f(H)*p_H = S_f(L)*p_L$).

Figure 6.6 Simple three-step model describing constraints on the trade-off between energy intake and predation risk placed on individuals that achieve low energy intake while foraging intertidally. (a) food-based survival (S_f) is positively related to energy intake ε and will be greater if a topping-up feeding strategy *H* is employed rather than exclusive intertidal water feeding at low water *L*. (b) After the incorporation of survival constants p_L and p_H for strategies *L* and *H* respectively, individuals that achieve low energy intake during intertidal feeding maximize their overall survival by feeding supratidally over high water. (c) the importance of choosing the correct strategy (i.e. the difference in S between the two strategies) is greater for individuals of low and high ε, although foragers achieving a very low energy intake will have an extremely low overall *S* anyway.



6.4.3 Conclusion

Gould & Lewontin (1979) famously warned against considering purely adaptationist explanations for the characteristics of organisms. Here I show the importance of considering constrained explanations when trying to understand how animals distribute themselves in relation to food supply. In many cases, it may not be adequate to view such a system in terms of an adaptive trade-off between simple imperatives without considering the wider picture of individual constraints such as foraging efficiency or social costs to movement. A purely adaptive view of "alternative" foraging strategies would interpret the phenomenon as a simple fitness-indifferent response to the choice between low energy low predation risk and high energy high predation risk foraging patches. When individual variation in energy intake and costs to itinerancy are considered, the system is seen in the light of constraints leading to reluctant compensatory foraging.

This work has implications for the interpretation of any situation where we are tempted to impute fitness indifference to individuals, populations and species where "alternative" strategies are observed. Simple models can be used to incorporate the fitness inequalities arising from the cryptic (to the observer) acceptance of increased costs to following one or other of the strategies. Risk of predation is important in determining the distribution of foragers, but as shown here, individuals may vary in their opportunity to moderate this risk, and individuals must integrate several types of cost and benefit.

Chapter 7 - General Discussion

7.1 Feeding decisions by ruddy turnstones

This study has demonstrated that supratidal feeding appears to play a very different role in rocky shore systems than in soft-sediment systems. The likelihood of an individual going on to use high-risk supratidal habitats over the high water period appeared to depend not on supratidal resource availability, but on social constraints and events that occurred while the forager was using intertidal habitats. Foragers that frequently used supratidal substrates tended to be higher ranking, older, and more narrowly-ranging. However, this is a field-based study, and it is difficult to establish cause and effect. Birds may attain high rank by virtue of remaining highly site faithful rather than the other way around. At this stage, it is not possible to suggest relative fitness values for birds adopting different approaches to supratidal foraging. These results indicate that we are certainly not looking at a simple "topping-up" system in which poor quality foragers compensate for inadequate intertidal energy intake by feeding supratidally. The decision to feed supratidally is also affected by the interplay of other factors including predation risk and social status.

Relatively stable intertidal resource dynamics appear to be the ultimate reason why soft- and hard- substrate systems work in different ways. Stable resource dynamics mean that high ranking birds can remain highly site-faithful within and between years. However, despite the general stability of intertidal habitats, there will be some variation in intertidal habitat quality within and between winters. Because the spatial response to this variation by site-faithful birds is constrained for social reasons, they must use additional supratidal resources. It is worth these birds paying the cost of elevated predation risk in the short term for the long term benefits of a stable social system and associated benefits of stable group living. An analogous system operates in alpine choughs *Pyrrhocorax graculus* (L.), where foragers in

groups pay short-term costs in foraging efficiency for the long-term benefits associated with maintenance of social bonds (Delestrade 1999).

In this study I demonstrated that naturally-occurring supratidal foraging patches were much more profitable in terms of energy intake per unit time than intertidal patches. An average prey item in beach-cast wrack contained three times more energy value than an average item in intertidal habitats, and a forager continuously using beach-cast wrack needed to forage for 2.4 hours less per day than a bird using *Fucus*-covered rocks continuously. Despite this apparent energetic advantage to supratidal habitats, foragers were reluctant to use them, and were clearly not distributing themselves in proportion to available food, as would be predicted from an ideal free distribution model (Fretwell & Lucas 1970). Moreover, flocks that were found on supratidal habitats maintained a higher level of vigilance than would be predicted from their flock size alone, while flocks on intertidal habitats were less vigilant than expected. This suggests that a high perceived risk of predation was the reason why ruddy turnstones were reluctant to use supratidal habitat patches. The use of supratidal habitats in this study system appeared therefore to represent a direct trade-off between the risks of starvation and predation.

The decision to feed supratidally was not driven by the availability of supratidal resources, suggesting that some ruddy turnstones fed supratidally, usually over the high water period, because they had not fulfilled their energy intake requirements while feeding intertidally during the low water period. This has been shown before in soft-sediment systems (Velasquez & Hockey 1992, Goss-Custard et al. 1996, Dann 1999, Masero et al. 2000, Masero & Pérez-Hurtado 2001). In these systems, individuals of low foraging efficiency are thought to be forced into continuing to forage when intertidal habitats are unavailable. Furthermore, supratidal habitats used by oystercatchers were poorer in quality than intertidal habitats, and also thought to elevate parasite burden. In this sense, supratidal foraging incurs two costs; the extra foraging time needed to fulfil energy requirements, and an increase in parasite burden. My work suggests that predation risk should now be considered an

additional cost of feeding supratidally. In all the systems so far studied, the prevailing current interpretation of supratidal feeding is that poor quality birds are forced into paying additional costs to extend their daily foraging beyond the period when intertidal habitats are available, such as parasite burden, increased time spent foraging, and predation risk.

Here, I studied a rocky shore system, in which intertidal resources were much more predictable than in soft-sediment systems. Resource predictability may be one of the factors that led to the evolution of a stable and complex social structure in populations of non-breeding ruddy turnstones. Individual ruddy turnstones pay a high cost in terms of access to predictable resources if their position within the dominance hierarchy is supplanted (Whitfield 1990). Not unexpectedly, therefore, higher ranking birds tend to have smaller home ranges than lower ranking birds (Metcalfe 1986, Eaton 2001). However, foraging success depends not only on individual quality, but also on the forager's energy and nutrient requirements, long term changes in food availability, extrinsic factors such as weather conditions, and the forager's ability to compensate for these factors by spatially tracking the best current foraging areas.

In this study, higher ranking ruddy turnstones, and males independently of rank, tended to feed supratidally more frequently than lower ranking and female birds. These birds pay the cost of increased predation risk associated with supratidal feeding, but have the benefit of retaining their position in a socially complex environment. Moreover, as is frequently the case with high ranking individuals, their risk of starvation is relatively low because they gain and defend access to predictable intertidal foraging areas (Clark & Ekman 1995, Hake 1996, Pravosudov et al. 1999). However, their risk of predation is relatively high because in times of depressed intertidal food availability, they are forced to continue feeding over high water, thereby exposing themselves to elevated risk of raptor attack.

Lower ranking birds are less attached to specific foraging areas, and so range more widely during the course of the winter. Because they can

respond to variation in intertidal food supply by seeking new foraging areas, they need to supplement daily energy intake through supratidal feeding less often than more narrowly ranging birds. These birds pay a cost of increased travelling time and energy expenditure, and never have access to the best intertidal foraging sites in any given area. Therefore, they run the risk of starvation. However, their risk of predation is lower than more narrowly ranging birds, because they need to feed supratidally less frequently.

As with other systems studied so far, the proximate cause of supratidal feeding in ruddy turnstones appears to be inadequate energy intake while foraging intertidally. However, the ultimate causes for the patterns of variation in supratidal feeding uncovered in this study appear to be very different. The birds feeding supratidally were not necessarily poor quality birds, rather those that had limited opportunity to respond spatially to variation in food availability.

7.2. The benefits of site fidelity and the costs of movement

Close spatial associations with particular sites or social groups can affect how foragers solve trade-offs such as that between intake rate and predation risk. For example, although adult striped bass *Morone saxatilis* (Walbaum) perform better at low water temperatures, they showed no change in site fidelity during the non-breeding season despite large spatial variation in water temperature (Jackson & Hightower 2001). The fish were apparently prepared to sacrifice physiological performance (presumably increasing their risk of predation) for benefits associated with site fidelity. Maintaining site fidelity makes sense in situations where there are strong benefits to group living, such as a stable resource base best exploited by high ranking individuals (Krause & Ruxton 2002). It may be worth paying a cost of e.g. additional predation risk for the reduced variance in energy intake rate through continuous access to good quality foraging sites. This hypothesis predicts that variance in energy intake during intertidal feeding in ruddy turnstones should increase with dominance status, something that could be tested in further study.

High ranking ruddy turnstones in this study showed high site fidelity and fed more frequently on supratidal habitats than low ranking birds. This indicates that the more mobile birds are doing something that allows them to reduce the amount of time they spend on high risk supratidal habitats. It is likely, therefore, that they are switching to higher quality intertidal habitats following a decrease in food availability in the current area. It does not appear that wide-ranging birds are tracking the occurrence of ephemeral supratidal habitats (Eaton 2001) because (a) upon quantitative spatial analysis, these habitats were found to be spatially rather predictable and (b) wide-ranging birds travelled the same distances to supratidal habitats than did narrow-ranging birds.

A further benefit of site fidelity in ruddy turnstones may be migrational synchronicity. Arrival time on breeding grounds in Greenland exhibits little variation despite some variability in spring weather, and occurs usually around late May to early June, highly stereotyped in particular areas (Manniche 1910, Nettleship 1973). Birds arrive in southern regions of Greenland from about 23 May, and reach the north coast by the first week of June (Bent 1929, Salomonsen 1950). Spring departure from staging sites in Iceland falls similarly within a very narrow time window between 25 May and 1 June, and is remarkably constant from year to year (Meltofte 1985, Alerstam et al. 1986, 1990). Ruddy turnstones have no way of predicting weather conditions so far from their starting point, so birds must rely on social synchronisation to time arrival using endogenous cues (Alerstam et al. 1990).

This high degree of synchronisation in migration and return to the breeding grounds may be achieved in part through the high group cohesiveness and site fidelity seen in this species during the non-breeding season (Sutherland 1981, Cramp & Simmons 1983, Whitfield 1985a). Conventionally, winter site fidelity has been explained in terms of resource use during the non-breeding season (Metcalfe & Furness 1985, Burton & Evans 1997), but an additional benefit may be the achievement of breeding ground arrival synchronicity, of great adaptive consequence given the narrow time window for breeding in

such northerly latitudes (Green et al. 1977). The period immediately after hatching must coincide with maximum food availability (Nettleship 1973). This idea predicts a positive relationship between site fidelity and group cohesiveness, at both individual and population levels. Itinerant individuals might be part of less cohesive groups than highly resident individuals. At the population level, this idea could be tested by looking at winter site faithfulness in southern breeding (Fenno-Scandian) birds, where the time window for breeding is wider than northern Greenland. This study has shown that extreme site faithfulness during winter may carry the cost of reducing a bird's ability to cope with spatial variation in food availability.

For high ranking birds, the costs of movement to compensate for variation in habitat quality appear greater than the costs of increased predation risk by staying put. Movement between sites by wintering ruddy turnstones are likely to result in lost foraging opportunities, in particular because of the time taken to identify intertidal areas of higher quality than the one they left. These costs will multiply with distance travelled. Indeed, translocated orb web spiders *Metepeira incrassata* paid increasing foraging opportunity costs the further they were moved, and this is likely to be a frequent pattern across many taxa (Jakob et al. 2001).

7.3 Implications for foraging theory

Although specific costs and benefits associated with alternative foraging decisions can be modelled explicitly and investigated experimentally, the interactions among different types of costs and benefits can be very hard to observe. More importantly, these interactions can completely obscure or reverse some relationships predicted from necessarily simplified modelling or well-controlled experiment. This study has demonstrated two novel effects of this kind, both of which have implications for foraging theory. I have shown that variation in predation risk can disrupt the group size effect (chapter 4), and that position within the dominance hierarchy can affect the solution to the trade off between the risks of starvation and predation, by leading to spatial constraints on ranging behaviour (chapter 6).

The results of this study highlight the complexity of in-the-field decisions made by foraging birds, and the difficulty of interpreting observational data on the distribution patterns of foragers. During the early stages of this study, I interpreted this system as a simple trade off between starvation and predation, with birds of low foraging efficiency being forced into paying additional costs of predation risk by foraging supratidally, as is the case in the soft-sediment systems studied so far. I assumed these birds would also range more widely to keep track of patchy and ephemeral supratidal food resources. However, as I began to uncover the spatial strategies of persistent supratidal foragers, and realised that these birds were in fact higher ranking than intermittent supratidal foragers, it became clear that there was a substantial cost of movement to new intertidal foraging sites within and between winters, particularly for high ranking birds. This study has shown that the consequences of dispersive movements depend on social status.

There is little information on the ontogeny of movement patterns over the lifetime of individuals (but see Townshend 1985). I was unable to detect age effects in this study owing to small sample sizes, but the balance between the costs and benefits of site-fidelity is likely to change over an individual's lifetime. This is particularly important for long-lived species such as the ruddy turnstone, and deserves further investigation.

7.4 Implications for conservation science

It is common to base conservation decisions on the relative importance of different habitats to organisms. On the basis of the traditional assumption that ruddy turnstones are rocky shore specialist shorebirds, sandy beaches were excluded from the area designated as an SPA (Anthony 1999, Stroud et al. 2001). Indeed, ruddy turnstones spend most of their time on rocky shore habitat. However, this study has highlighted the ecological importance of beach-cast wrack, which is usually deposited on sandy susbtrates. Although foragers spent relatively little time using beach-cast wrack, it was important ecologically as a foraging resource for narrow-ranging birds. Therefore, when

considering the relative importance of different habitats used by animals, it is essential to consider not just how long an animal spends in alternative habitats or how much of its home range overlaps particular habitat types, but the functional role of the different habitats used. Studies prioritising areas for conservation will make inappropriate recommendations if the ecological importance of alternative areas is overlooked.

It has been suggested that changes in the frequency that shorebirds feed supratidally may reflect changes in intertidal habitat quality (Tsai 2001, Smart & Gill 2003). However, this study has shown that we must understand the causal basis of supratidal feeding before using it as an index of habitat quality. Individual ruddy turnstones may respond to deteriorating intertidal habitat quality not by foraging more frequently on supratidal habitats, but by ranging more widely along the coast both within and between winters to track intertidal resource quality. This may or may not be associated with increased levels of supratidal foraging.

7.5 Implications for organic pollution policy

As stated in the introduction, improved levels of treatment applied to sewage effluent before discharge into the study area are likely to lead to falling nutrient levels over coming years. The literature on the effects of organic pollution on marine environments is large, and the general picture is of benefits for species diversity and abundance at moderate levels of enrichment (Pearson & Rosenberg 1978). Species involved include molluscs and polychaetes (Anger 1975). As organic inputs increase still further, both species diversity and biomass decline, as body sizes become smaller and the fewer highly opportunistic species begin to dominate. However, it is likely that organic enrichment in the present study area is no more than moderate, as it is classified as an area of high natural dispersion (Hiscock 1998).

Few studies have been carried out on rocky shore habitats; much of the above information is based on estuaries and using soft-sediment dwelling invertebrates (but see Littler & Murray 1975, 1977, Gappa et al. 1993, and

Rogers 1999 for important exceptions). Shelled organisms found in rocky intertidal habitats may be able to buffer some of the effects of organic enrichment through greater control over water transfer than soft-bodied invertebrates.

Several studies have related bird numbers to organic pollution events (see Green et al. 1993 for a comprehensive review for estuarine systems). The general pattern is for reduced prey populations to lead to depressed shorebird numbers, but it must be borne in mind that improved water quality has many other benefits (EEC 1976, Obiri-Danso & Jones 1999).

Since sewage treatment began in 1977, sea duck populations in the Firth of Forth, formerly concentrated around sewage outfalls (Milne & Campbell 1973) declined steeply. Species particularly affected were greater scaup *Aythya marila* (L.) and pochard *Aythya ferina* (L.), although mallard *Anas platyrhynchos* L. and teal *Anas crecca* L. also declined. Red knot and dunlin *Calidris alpina* (L.) at Kinneil declined following foreshore reclamation works and changes in patterns of effluent disposal, although ruddy turnstone numbers increased in the Firth of Forth over the period. Effects of national trends were removed from these data, and changes in sewage treatment regimes overall since 1977 were implicated in reducing the importance of the Firth of Forth as a wintering area for shorebirds and wildfowl (Bryant 1987).

The only study explicitly to cite organic pollution as a probable cause of increase in bird populations is that of van Impe (1985). Organic pollution to the Western Scheldt estuary in The Netherlands has increased markedly since the 1950s, during which time populations of sediment-dwelling invertebrates also rose, with an associated decline in species diversity. Bird populations also increased dramatically over the period, although national trends were not reported, and the importance of immigration as a product of deterioration of other sites is not discussed fully.

Much of the evidence gathered to date is necessarily of a correlational nature, and does not demonstrate a causal link between changes in effluent

treatment regimes and bird populations. Any such causal link is likely to be convoluted, owing to the complex and variable nature of littoral ecosystems, and the difficulty of quantitatively studying trophic and nutrient pathways. This is particularly true in the present study system. Even if we accept that diversity and abundance will decline in the study area, the potential impact on the ruddy turnstone population is unclear.

There is no evidence to suggest that the population is near the carrying capacity of the environment (Eaton 2001), and energy intake appears to be more limited by individual variation in foraging efficiency and trade-offs associated with predation risk and social status. However, it would be interesting to study this population again in 15 years' time to look for correlates of environmental change. We might predict fewer and smaller deposits of beach-cast wrack and because of this, increased itinerancy by ruddy turnstones as birds are forced to range more widely. We might also expect lower stability of social groups, possibly leading to fitness impacts on the population.

7.6 Where next?

The thrust of this work has been to reveal some of the patterns in ruddy turnstone foraging behaviour in a field setting. As with any study of an unmanipulated natural system, it is difficult to reach firm conclusions about causality. The next steps in this research programme must include manipulations to isolate various components of foraging decisions by these birds and provide experimental underpinning.

Perhaps the most important next step is to quantify predation risk in the different parts of this system. We need to demonstrate empirically that predation risk is greater for foragers on supratidal habitats than on intertidal habitats, and in particular foragers on beach-cast wrack. Predation risk while roosting is also an important quantity. This will involve lengthy observations of shorebird flocks and documentation of predator attacks. An alternative approach is to vary predation risk experimentally in a field setting using

flyovers of trained raptors and then looking for effects on vigilance behaviours and the propensity to feed supratidally.

Given suitable manpower and resources, the size, quality, and predictability of beach-cast wrack deposits could be manipulated in the field. Foraging decisions could then be related experimentally to spatial and temporal resource dynamics. This would be interesting because this system allows experimental manipulation of a naturally patchy and ephemeral resource. Many foraging experiments, even if based in the field, have used unrealistic set-ups involving artificial apparatus for manipulating resource dynamics.

It would be interesting to relate individual differences in risk-management strategies to supratidal feeding. Lima & Bednekoff (1999) predict that where high risk situations are rare, foragers should show greatest antipredator behaviour when on a high risk substrate, and that this antipredator behaviour must necessarily decline as high risk situations become commoner. In the current system we might predict that persistent supratidal feeders will show less vigilance on average than intermittent supratidal feeders.

Ruddy turnstones appear to be limited to diurnal foraging, and thereby forced to use high risk habitats to compensate for variation in intertidal energy intake. We might therefore predict a latitudinal gradient in supratidal foraging by ruddy turnstones, driven by the poleward reduction in winter daylength. Ruddy turnstones winter across much of the globe, so they present an ideal opportunity for study, particularly as birds wintering in the southern hemisphere will experience very long daylengths in comparison with those wintering in the north. Current information on supratidal feeding by shorebirds is too scattered and methods not comparable, so further quantitative field study would be necessary. There is some support in the literature for the idea of a latitudinal gradient in supratidal feeding. Working in California, Fleischer (1983) reported that no ruddy turnstones fed supratidally, while at high latitudes in Europe, several shorebird species regularly feed supratidally (Goss-Custard et al. 1996, Smart & Gill 2003).

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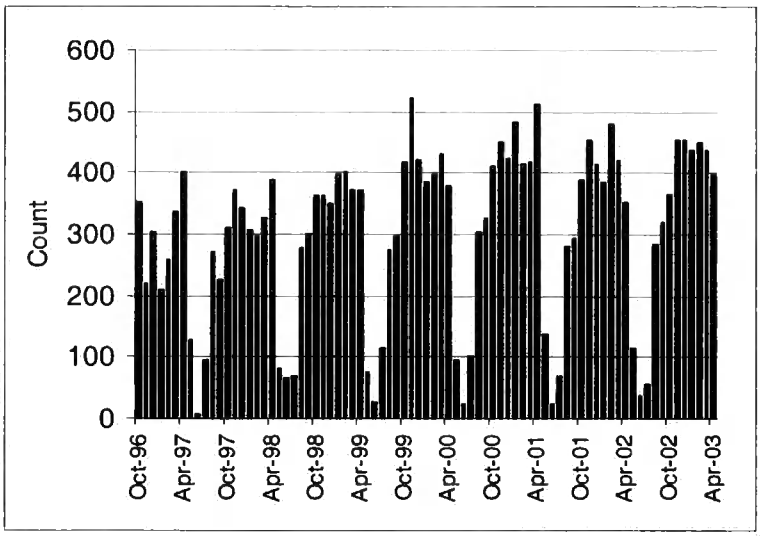
Appendix 1. Study population and general methods

A1.1 Study population

The study site comprised a 39.5 km stretch of rocky coastline in north-east England (see chapter 1 for physical characteristics and descriptions of habitats). Fieldwork for this study was conducted bewteen October 1999 and March 2003. The wintering populations of ruddy turnstones and purple sandpipers in north-east England are of international importance. Over 1400 ruddy turnstones regularly spend the non-breeding season in the Northumberland Shore SPA, the large protected area comprising much of the coast of north-east England and wholly encompassing the study area (five year peak mean 1991/2 - 1995/6; JNCC 2001). The population within the study area itself is approximately 500 birds (seven year peak mean 1996/7 - 2002/3 = 499; figure A1, Eaton 2001). Monthly maxima for 1969 – 1976 presented by Prater (1981) suggest about 350 ruddy turnstones used the area between Whitley Bay and the Coquet Estuary during that period. The difficulty of counting shorebirds on rocky coast habitats makes a detailed historical analysis of population trends impossible, although data on winter maxima published anecdotally in *Birds of Northumbria* since 1970 appear to indicate that shorebird populations have remained stable in the study area over the past 30 years, against a background of a national decline (Cranswick et al. 1999).

Count data collected by Eaton (2001) and as part of this study indicate that the highest numbers of birds are present between October and April, with a few birds oversummering each year (figure A1). A detailed analysis of the data presented here are beyond the scope of this study, and they are only shown to give an impression of the numbers of birds using the study area over the course of the year.

Figure A1. Average monthly counts of ruddy turnstone present in the study area between October 1996 and April 2003. Data prior to October 1999 taken from Eaton (2001).

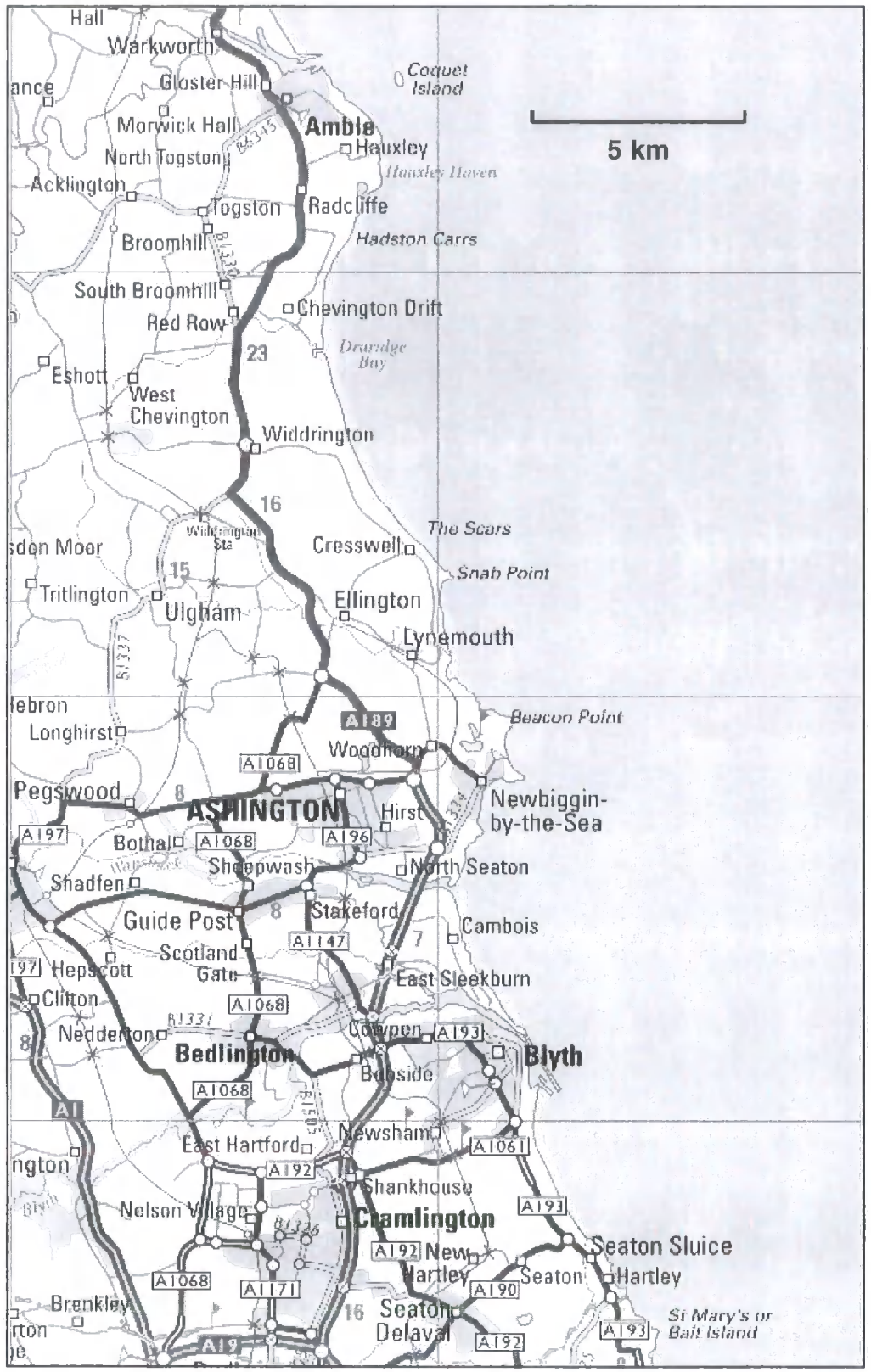


A1.2 Counting birds: general methods

Good road access to the study area greatly facilitated the counting of birds over a wide area relatively quickly. With the exception of Newbiggin, where a 20 minute walk was required to view all roosting and feeding sites up to Beacon Point (see figure A1), all parts of the shoreline were visible from vantage points within a few minutes' walk of a vehicle. Counts of all shorebirds in the study area were made twice a month as part of a study monitoring the effects of changes in nutrient discharges into the nearshore environment.

Where a count had to be achieved within a single high water period (defined as two hours either side of the time of high tide), counting always commenced at the northern end of the study area and proceeded southward. This took advantage of the 20-minute delay in tidal flow from the northern to southern end of the study area. Vantage points allowing a clear view of all exposed habitat along the shoreline were visited, and all fields within 500 m of the coastline were checked during each count period. Counts were usually completed within four hours.

Figure A1. Map of the study area showing access roads.



A1.3 Catching and marking birds for study

Ruddy turnstones were caught using cannon-nets at Amble, Hauxley, Cresswell, Newbiggin and St Mary's Island between 5 February 1997 and 26 October 2000. Catches were generally accomplished by firing the net over groups of birds foraging on beach-cast wrack deposits. To minimise bias caused by catching birds only when feeding over high water, sampling was only carried out on occasions where a high proportion of the population was high water feeding. Birds were ringed with a combination of coloured plastic rings and a metal ring, totalling four or five rings on each bird. The scheme was designed to allow birds to be resighted in the field, so bright and easily distinguished colours were chosen (green, lime, orange, red, white, yellow). All rings were fitted on the tarsus, except where four coloured rings were used, in which case the metal ring was fitted on the tibia and all four coloured rings on the tarsus. Birds showing distinct pale buff fringers on their inner median coverts were aged as juveniles (Prater et al. 1977). However, the usefulness of these feathers in diagnosing juveniles declines after November, and many birds not showing buff fringes to the median coverts could not be aged with certainty.

Over 11 attempts, a total of 229 birds was caught by cannon-netting and colour-ringed. This represents over 40% of the ruddy turnstone population in the study area. Average catch per sampling session was 20.8 birds (range: 2 - 50). Twenty-three birds were aged with certainty as juveniles, only 10% were aged with certainty as juveniles, although as explained above, some juveniles were probably overlooked.

A1.4 Resighting birds: general methods

Resighting data were collected opportunistically while carrying out other parts of the fieldwork schedule. Resighting data were collected on 349 dates between 10 February 1997 and 16 November 2002. Mean height of high tide on dates where resightings were made did not differ significantly from mean high tide height of all dates during the study period ($t = 0.35$, d.f. = 2452, $p =$

0.726), indicating that resampling of birds was carried out randomly with respect to magnitude of tide. A mean of 14.4 colour-ringed birds was resighted each day in the field (range: 1 - 72). On only 7% of occasions was a bird resighted more than twice in a day, helping to minimise temporal autocorrelation in the dataset.

Appendix 2

Characteristics of the 50 deposits of beach-cast wrack observed during winter 2000/2001. Where measurements were taken from a particular deposit more than once, the data are averaged. * indicates data not collected or could not be calculated. Weeks are numbered consecutively from the first week of November. See chapter 2 for analyses.

ID	Lifespan (weeks)	Week appeared	Length (m)	Volume (m^3)	Surface area (m^2)	Temp (ºC)	Estimated total Coelopids (*10,000)	Estimated maximum Coelopids l^{-1}
1	6	1	84.2	61.1	381.4	13.8	2295.1	85545.9
2	1	1	16.0	1.5	17.3	*	*	*
3	5	1	108.0	187.6	592.1	14.8	3768.6	192919.2
4	4	1	25.0	12.3	90.5	8.2	4.6	16.5
5	6	1	51.0	75.6	300.9	13.1	91.5	895.9
6	1	1	10.0	1.3	21.2	*	*	*
7	1	1	36.0	2.7	35.2	*	*	*
8	2	1	41.0	30.8	154.9	8.8	10.4	15.2
9	1	1	41.0	4.5	63.9	*	*	*
10	1	1	90.0	102.8	1011.5	*	*	*
11	6	1	58.3	177.9	377.7	11.3	292.9	17142.0
12	1	1	30.0	47.0	225.1	*	*	*
13	1	1	80.0	17.4	205.5	*	*	*
14	4	2	45.0	61.0	171.6	9.3	29.8	2219.6
15	1	2	100.0	433.5	978.3	8.9	64.2	19.6
16	1	2	30.0	5.7	62.8	8.7	4.0	14.7
17	1	2	20.0	11.5	84.4	9.1	5.8	20.3
18	1	2	10.0	1.9	19.3	*	*	*
19	1	3	70.0	29.7	242.9	6.5	10.6	10.2
20	5	3	52.0	30.9	178.9	10.0	2300.2	170318.8
21	1	3	60.0	10.9	127.8	6.9	6.1	13.8
22	1	3	40.0	16.8	142.5	6.7	6.4	10.2
23	3	4	30.0	20.7	189.5	9.7	16.9	64.2
24	2	5	90.0	38.6	307.5	9.9	25.3	23.1
25	2	7	35.0	16.6	215.8	4.1	7.1	6.0
26	6	7	76.7	58.2	281.6	12.0	466.7	13593.0
27	5	8	48.0	24.5	170.1	8.9	45.4	1383.4
28	1	8	50.0	14.5	125.3	8.5	7.8	29.0

29	1	8	70.0	70.6	229.3	8.6	15.3	38.9
30	1	8	40.0	70.5	171.9	7.9	9.0	13.0
31	2	8	40.0	22.3	186.7	6.5	6.8	8.2
32	2	9	90.0	55.1	370.5	5.2	12.0	5.7
33	1	9	50.0	81.8	281.4	5.4	9.4	7.3
34	1	9	30.0	10.5	90.5	4.8	2.8	4.5
35	1	9	20.0	47.3	203.4	5.3	6.7	5.3
36	2	9	110.0	47.3	329.6	5.3	10.9	6.4
37	2	9	60.0	94.4	339.8	5.7	12.2	6.4
38	2	9	125.0	144.0	471.0	5.7	17.3	6.9
39	4	9	47.5	36.4	191.2	6.6	14.7	134.0
40	1	10	20.0	21.4	106.8	5.1	3.5	5.7
41	1	10	120.0	50.2	291.9	5.7	10.9	9.3
42	1	12	90.0	124.8	251.0	6.5	10.3	8.2
43	1	12	20.0	3.3	47.6	5.3	1.6	5.1
44	2	12	50.0	38.1	251.8	7.8	12.8	11.3
45	4	13	67.5	74.0	346.0	14.9	3586.6	292449.6
46	4	13	45.0	31.2	161.4	16.2	6041.2	546038.9
47	4	13	42.5	74.5	197.2	13.9	498.2	51352.3
48	1	15	20.0	3.6	27.1	6.7	1.2	8.0
49	2	15	80.0	118.0	350.1	9.1	20.3	70.9
50	1	15	50.0	35.6	165.9	6.5	7.0	8.2

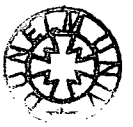
Appendix 3

Supratidal feeding and ranging statistics for the 140 colour-marked birds with sufficient data. See chapter 5 for analyses.

ID	Supratidal feeding frequency	Supratidal feeding likelihood	Range span (m)	Area of MCP (Ha)	Area of 95% fixed kernel	Number of cores in range	Partial area
1	0.23	0.69	23.42	3366.51	2468.25	2	0.42
2	0.34	0.74	3.65	260.52	122.09	2	0.23
3	0.2	0.83	3.78	246.03	145.78	2	0.2
4	0.28	0.79	30.55	3658.24	849.76	1	1
5	0.11	0.4	3.04	206.35	108.46	2	0.55
6	0.38	0.79	3.19	158.31	27.17	1	1
7	0.28	1	1.55	34.19	67.22	2	0.44
8	0.44	0.88	3.84	241.95	46.36	2	0.17
9	0.16	0.6	1.41	34.74	10.46	5	0.17
10	0.23	0.6	1.58	55.36	139.43	1	1
11	0.27	0.89	2.83	201.59	109.52	2	0.24
12	0.14	0.33	11.73	925.39	333.51	1	1
13	0.32	0.75	3.22	149.15	78.16	2	0.18
14	0.26	0.88	3.19	293.47	71.82	2	0.41
15	0.36	0.67	1.92	28.96	93.48	2	0.27
16	0.32	0.93	4.12	406.21	192.11	1	1
17	0.15	0.46	4.12	469.69	253.89	4	0.18
18	0.1	0.75	11.71	960.89	321.93	1	1
19	0.5	0.89	2.63	129.13	12.76	1	1
20	0.29	0.8	1.69	119.49	145.78	1	1
21	0.37	1	2.82	159.27	109.91	2	0.21
22	0.21	1	1.73	62.35	17.57	2	0.26
23	0.31	0.8	2.44	68.01	159.21	2	0.27
24	0.22	0.81	30.56	1825.41	688.16	1	1
25	0.5	1	30.36	3098.77	1126.99	2	0.42
26	0.23	0.73	2.72	137.27	92.85	1	1
27	0.31	0.73	30.3	4357.36	1384.49	2	0.25
28	0.29	0.8	11.63	643.91	173.33	1	1
29	0.13	1	2.53	104.11	72.2	2	0.14
30	0.17	0.67	2.4	98.45	7.49	1	1

31	0.26	0.86	3.49	389.49	193.34	1	1
32	0.24	0.8	2.79	138.98	91.4	2	0.14
33	0.14	0.67	1.73	122.83	171.4	1	1
34	0.17	1	18.26	1817.29	1000.24	1	1
35	0.29	0.63	3.42	270.09	193.47	1	1
36	0.15	0.4	0.64	7.41	19.28	4	0.12
37	0.29	0.88	3.42	337.77	160.98	1	1
38	0.2	0.4	3.32	137.15	344.28	1	1
39	0.46	0.92	1.03	30.2	28.84	2	0.18
40	0.35	0.89	0.95	9.77	26.3	1	1
41	0.32	0.78	2	76.57	15.39	1	1
42	0.38	0.89	0.3	4.93	6.29	1	1
43	0.38	0.8	12.45	666.84	929.52	3	0.04
44	0.2	0.75	2	94.91	91.3	1	1
45	0.33	0.5	2.4	198.69	326.51	1	1
46	0.2	0.71	3.2	451.09	291.13	4	0.25
47	0.36	0.45	16.82	1676.41	595.54	2	0.11
48	0.3	0.75	2.59	15.01	65.43	1	1
49	0.26	0.75	1.84	71.61	38.67	1	1
50	0.21	0.67	3.34	231.51	242.46	2	0.26
51	0.23	0.57	3.62	417.41	257.28	2	0.65
52	0.25	0.76	2.98	172.51	55.44	1	1
53	0.31	0.73	1.06	24.01	17.57	1	1
54	0.44	1	1.79	54.71	149.8	1	1
55	0.33	0.78	3.62	208.71	29.36	1	1
56	0.18	0.6	3.29	341.83	257.28	3	0.31
57	0.15	0.71	2.78	61.31	83.75	1	1
58	0.18	0.53	2.31	177.33	66.18	2	0.26
59	0.18	0.9	3.11	198.71	66.64	2	0.3
60	0.28	0.72	2.78	212.45	56.77	1	1
61	0.33	0.74	1.35	21.97	14.89	1	1
62	0.33	0.88	0.72	14.11	9.2	1	1
63	0.32	0.77	13.19	891.72	195.05	1	1
64	0.25	0.53	3.62	268.99	117.57	2	0.18
65	0.28	0.6	3.44	366.51	112.63	1	1
66	0.2	0.67	3.55	284.81	512.52	4	0.21
67	0.26	0.7	3.62	233.51	78.12	3	0.12
68	0.2	0.69	11.93	394.31	100.04	1	1
69	0.14	0.75	11.75	1133.21	604.24	1	1
70	0.27	0.88	3.85	243.69	124.39	2	0.33

71	0.38	0.67	16.86	1242.11	1121.22	2	0.13
72	0.27	0.67	1.35	23.69	23.19	2	0.79
73	0.4	1	0.72	5.01	8.88	1	1
74	0.22	0.57	1.08	11.11	9.64	1	1
75	0.33	0.8	0.98	14.77	17.54	1	1
76	0.24	0.73	3.36	196.99	95.36	1	1
77	0.09	0.2	2.7	192.21	227.18	2	0.23
78	0.27	0.77	30.53	2843.41	564.78	1	1
79	0.28	0.56	28.48	2712.47	3387.99	1	1
80	0.34	0.75	1.95	121.41	14.84	1	1
81	0.25	0.59	13.19	2537.54	523.25	3	0.06
82	0.37	0.88	11.53	980.63	380.54	1	1
83	0.5	0.75	0.95	23.44	6.6	1	1
84	0.21	0.75	11.53	333.33	167.27	1	1
85	0.27	1	6.17	149.86	141.01	1	1
86	0.29	0.71	12.2	269.81	328.13	2	0.06
87	0.56	0.9	7.75	151.61	76.19	1	1
88	0.25	0.63	1.84	37.41	40.29	1	1
89	0.6	0.9	11.45	256.84	192.91	1	1
90	0.5	0.86	12.19	222.49	388.35	1	1
91	0.14	0.38	15.74	1887.63	962.68	2	0.22
92	0.52	0.93	12.05	1246.93	954.02	3	0.06
93	0.44	0.88	1.84	49.51	58.59	1	1
94	0.28	0.69	12.52	1212.51	234.41	2	0.13
95	0.37	0.86	3.27	183.91	132.9	2	0.5
96	0.36	0.71	4.17	507.5	174.88	1	1
97	0.32	0.82	3.18	313.61	151.51	1	1
98	0.36	0.89	2.55	143.11	140.54	2	0.41
99	0.29	0.82	2.71	157.71	87.07	2	0.46
100	0.16	0.57	17.2	2534.41	981.69	2	0.32
101	0.21	0.56	2.55	172.11	205.06	3	0.15
102	0.36	0.69	11.29	435.06	182.89	1	1
103	0.1	0.67	5.22	427.31	150.34	1	1
104	0.14	0.36	3.92	376.13	159.5	1	1
105	0.36	0.67	2.55	135.61	72.86	2	0.32
106	0.3	0.75	3.92	507.21	206.72	1	1
107	0.3	0.74	3.56	428.87	154.13	1	1
108	0.22	0.69	3.35	208.71	144.3	4	0.15
109	0.34	0.78	3.16	209.67	156	3	0.24
110	0.23	0.7	3.8	317.83	126.74	3	0.2



111	0.25	0.82	11.57	727.61	250.59	1	1
112	0.21	0.76	11.56	1356.35	299.45	1	1
113	0.25	0.75	2.66	150.74	91.39	3	0.04
114	0.21	0.6	11.75	676.31	279.45	1	1
115	0.23	0.48	3.56	381.97	166.54	1	1
116	0.23	0.64	3.32	402.73	161.31	1	1
117	0.39	0.7	3.18	295.81	212.75	1	1
118	0.33	0.71	2.53	125.11	126.94	3	0.1
119	0.21	0.57	5.22	362.31	191.78	1	1
120	0.29	0.64	12.29	769.01	428.19	4	0.1
121	0.23	0.73	3.16	140.77	153.61	1	1
122	0.32	0.93	5.36	410.97	131.11	1	1
123	0.29	0.71	30.63	3369.79	1210.1	1	1
124	0.25	1	11.08	537.81	146.94	1	1
125	0.43	1	3.54	145.81	44.52	1	1
126	0.36	0.8	1.07	33.36	39.92	1	1
127	0.64	0.9	0.23	2.1	2.23	1	1
128	0.47	0.89	0.7	11.29	15.5	1	1
129	0.63	0.88	0.45	4.25	0.85	1	1
130	0.3	0.5	2.29	45.99	77.37	1	1
131	0.67	1	0.12	0.26	0.04	1	1
132	0.65	0.92	0.13	0.97	0.6	1	1
133	0.67	0.83	0.45	2.08	0.4	1	1
134	0.3	0.5	0.63	8.21	4.92	1	1
135	0.67	0.92	0.6	5.14	2.21	1	1
136	0.13	1	0.52	6.96	18.93	1	1
137	0.21	1	0.36	2.56	1.83	4	0.09
138	0.13	1	0.36	4.06	5.58	2	0.34
139	0.39	1	1.19	16.95	8.64	1	1
140	0.35	0.75	1.95	89.94	19.75	1	1